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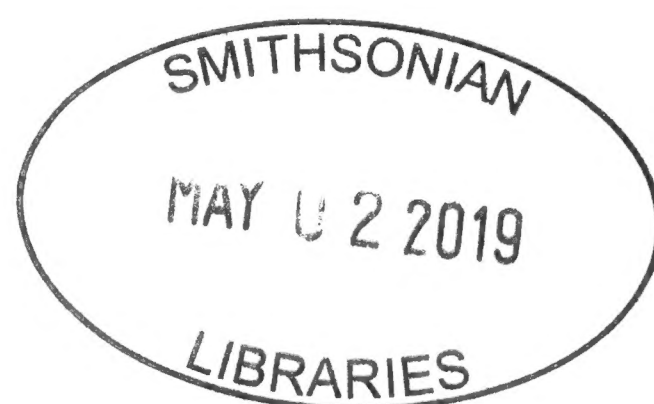
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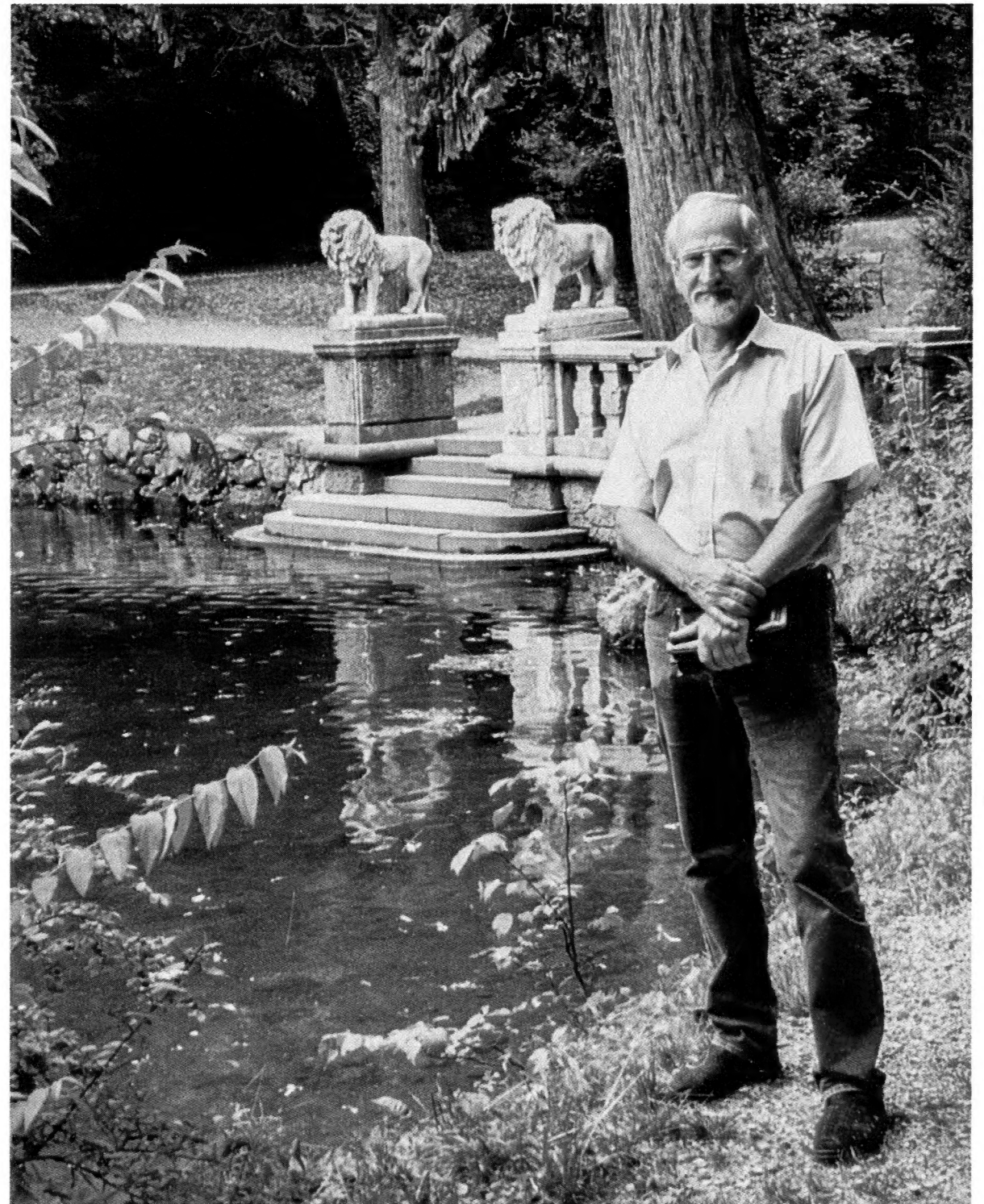
Volker Mahnert**3 December 1943 – 23 November 2018**

In the morning of 23 November 2018 Volker Mahnert, former director of the Natural History Museum of Geneva (MHNG) and former editor-in-chief of the *Revue suisse de Zoologie*, passed away in a Genevan hospital following complications after surgery. His family was at his side when he closed his eyes forever.

Volker Mahnert was born in Innsbruck (Austria) on 3 December 1943, the second of three sons of Klaus and Hanna Mahnert. His father was a businessman in Innsbruck, his mother (from an old family with Anglo-Irish roots) a housewife with a degree in economics.

Volker Mahnert attended grammar school (Bundes-Realgymnasium) in Innsbruck and subsequently intended to study medicine at the University of Innsbruck. Before that, however, he wanted to explore another part of the world – as one does at that age. He went to Hamburg (Germany), found a berth on a cargo ship and worked his passage to the USA. By the time he got back to Innsbruck after four months, he found he had missed the deadline to enrol at the Faculty of Medicine and so he enrolled at the Faculty of Philosophy and studied biology instead. During his student years he greatly enjoyed skiing and playing football (he considered going professional), and he became Tyrolian pole vault champion as a member of the Innsbruck athletics club. He was still keen on exploring also other parts of the world, and between semesters in 1965 he had the opportunity to visit British relatives of his mother in Nairobi, Kenya, where they ran a business. This family contact proved useful for expeditions to Kenya in later years. Being a zoologist in the making, he wanted to know how best to make scientific use of his first visit to a tropical country. What kind of animals should he collect there? Bernd Hauser (then assistant professor at the Institute of Zoology of Innsbruck University) suggested the pseudoscorpions, because Prof. Max Beier (1903-1979) at the Natural History Museum in Vienna would certainly be interested in them. Volker Mahnert followed this advice, and a fascination developed that lasted for the rest of his life.

In 1969 to 1970 he was employed as an assistant at the Institute of Zoology in Innsbruck whilst also working on a doctoral thesis on the ecto- and entoparasites of small mammals of his native Austrian province of Tyrol under the supervision of Prof. Heinz Janetschek (1913-1997).



Volker Mahnert in the park of Schloß Matzen (Matzen Castle; Tyrol, Austria), which was owned by his Anglo-Irish great-grandmother Frances M. C. “Fanny” Grohman, née Reade (1831-1908), a distant relative of the 1st Duke of Wellington, famous for defeating Napoleon in the Battle of Waterloo (photo A. Mahnert).

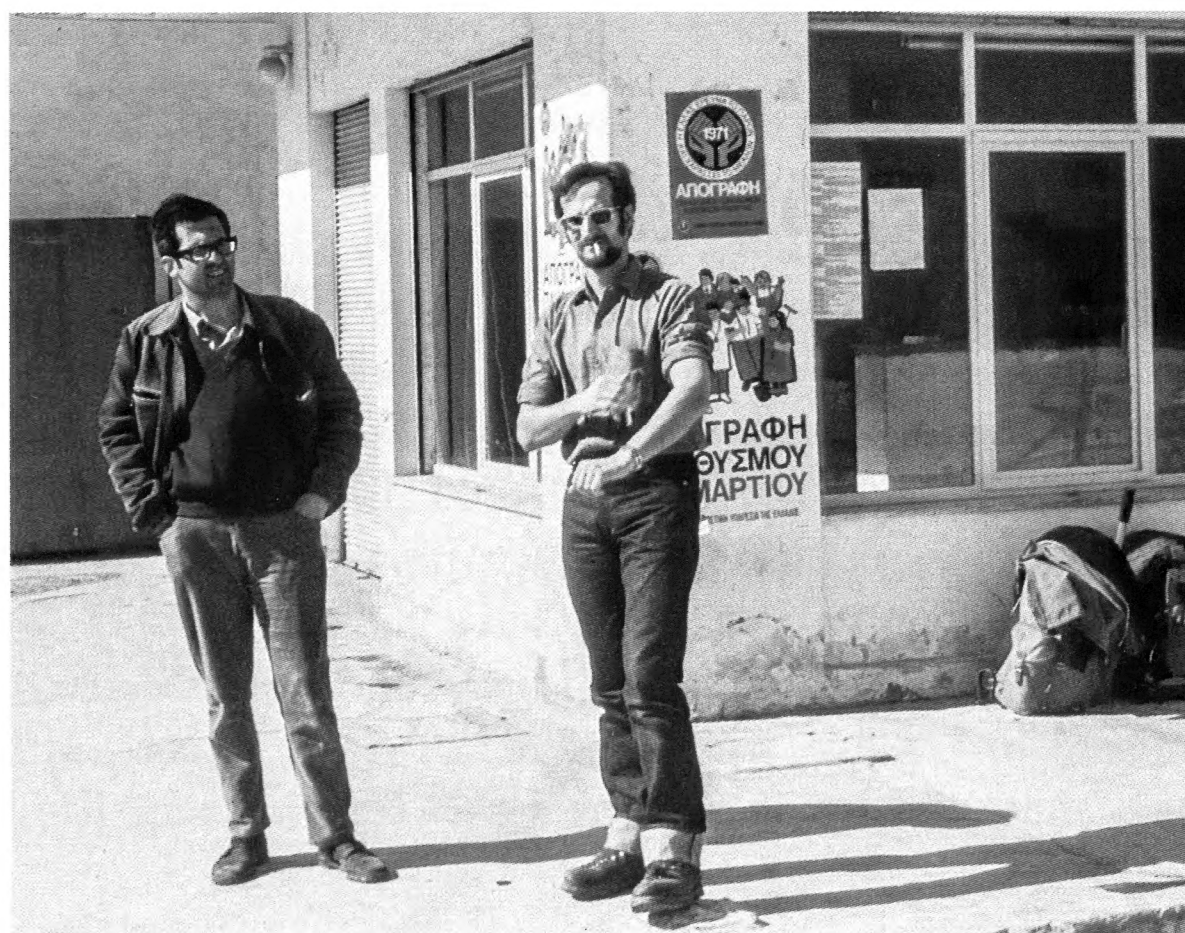
This study also involved an examination of protozoan blood parasites, which made it necessary to repeatedly consult with Dr Heinz E. Krampitz at the Institute of Tropical Medicine in Munich (Germany). In 1971 Volker Mahnert received his doctorate from the Faculty of Science of Innsbruck University. At the beginning of 1971 he was engaged by the Natural History Museum of Geneva as the curator of the Department of Herpetology and Ichthyology, succeeding Villy Aellen (1926-2000) who then became director of the museum. Volker Mahnert moved to Geneva with his fiancée, Anka Fiedler, and they married here on 22 May 1971. Together they have



Volker and Anka Mahnert (photo A. Mahnert).

a son and a daughter, Jan (born 1973) and Annick (born 1975). Upon arrival in Geneva, Volker Mahnert had no knowledge at all of the French language yet, but he learned it fast and he learned it well.

During his time as curator (1971-1989) he collected animals in the region and also went on several official scientific expeditions further away: Greece in 1971 (together with Bernd Hauser and Ivan Löbl), 1972 (with B. Hauser), 1973 (with B. Hauser and I. Löbl); Kenya in 1975, 1977 (with Jean-Luc Perret); Ivory Coast in 1980 (with J.-L. Perret); Paraguay in 1979 (with François Baud, Carlo Dlouhy, J.-L. Perret and Claude Vaucher), 1982 (with F. Baud, C. Dlouhy, J.-L. Perret and C. Vaucher), twice in 1985 (with F. Baud and C. Dlouhy; C. Vaucher and C. Dlouhy), 1990 (with Sonia Muller and C. Dlouhy). The Paraguayan expeditions were guided by Carlo J. Dlouhy (1933-2017), a Genevan who lived in that country for many years. Other trips (Italy in 1969, USA in 1998, Australia in 1992, Brazil in 1998, 2006) had



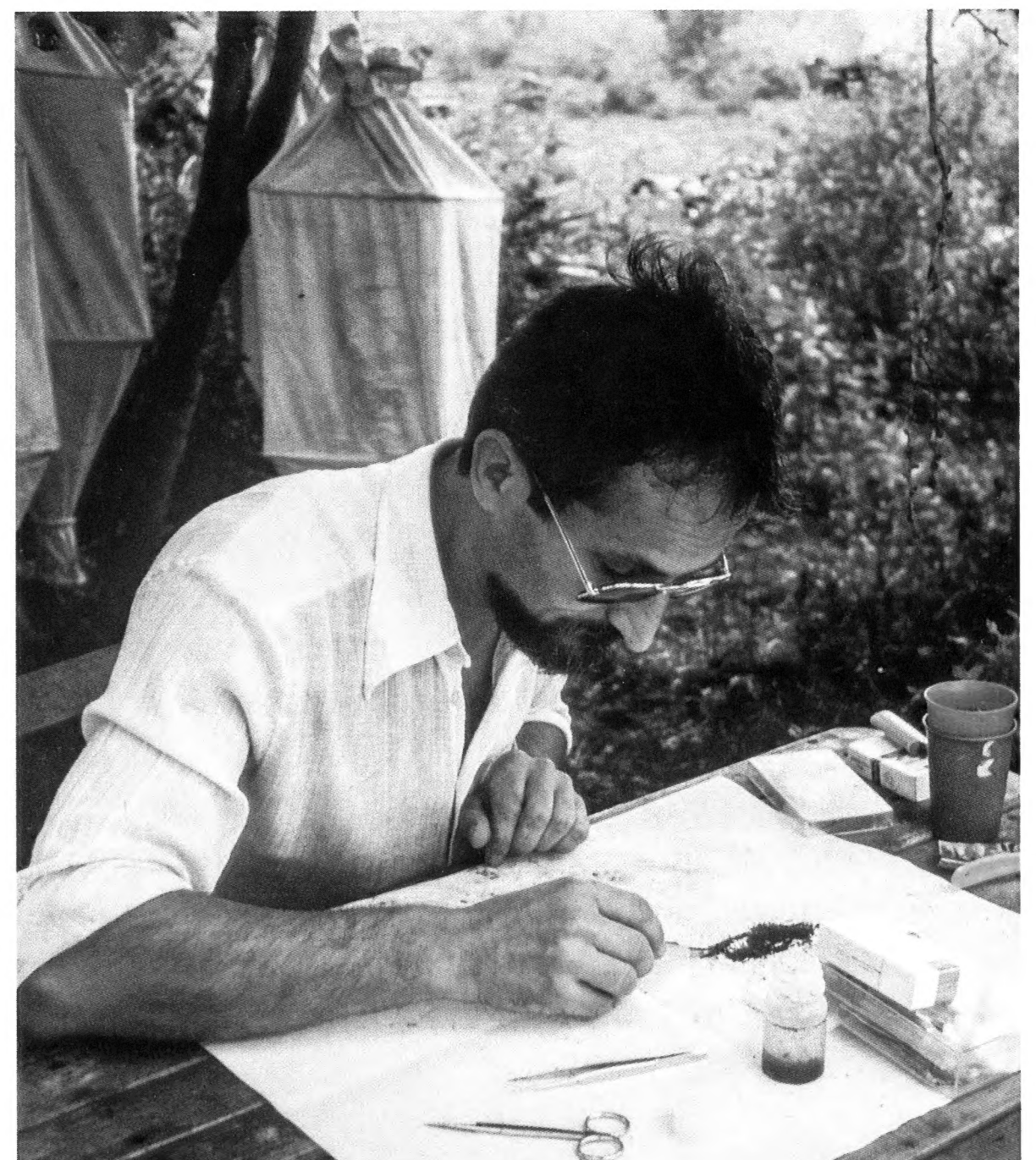
Volker Mahnert on his first zoological expedition as curator at the MHNG; together with Ivan Löbl (left) on the Ionian island of Zakynthos in 1971 (photo B. Hauser).

different purposes (scientific meetings, Ph.D. defences), but he always took the opportunity to collect. During all these trips he collected not only amphibians, reptiles and fish, as was expected of the curator of the herpetological and ichthyological collections, but also arthropods, and especially pseudoscorpions.

The years (1971-1989) when he was curator were his most productive in terms of scientific output (see appendix 1), spurred on by an amicable competition with Ivan Löbl (former curator of the Department of Entomology 2) for who could get more publications. It is such a pity that



Volker Mahnert chasing aquatic wildlife and being the attraction of village folks on Lefkada Island in 1971 (photo B. Hauser).



Volker Mahnert sorting specimens from a Winkler/Moczarski soil eclector in Paraguay (photo C. Vaucher).



Volker Mahnert in photo-ambush for fish gasping for air in Paraguay (photo C. Vaucher).

one of the contestants dropped out of the race much too early. Nevertheless the record is most impressive. Volker Mahnert has published 200 papers on various subjects and on a wide spectrum of animals, including blood-parasitic protozoans, endoparasitic worms and ectoparasitic arthropods, spiders (only peripherally), palpigrades, amphibians, reptilians, fish, mammals and, above all, pseudoscorpions. Two co-operations with close friends can be highlighted: on characiform fish with Jacques Géry (1917-2007) and on Brazilian pseudoscorpions with Joachim U. Adis (1950-2007).

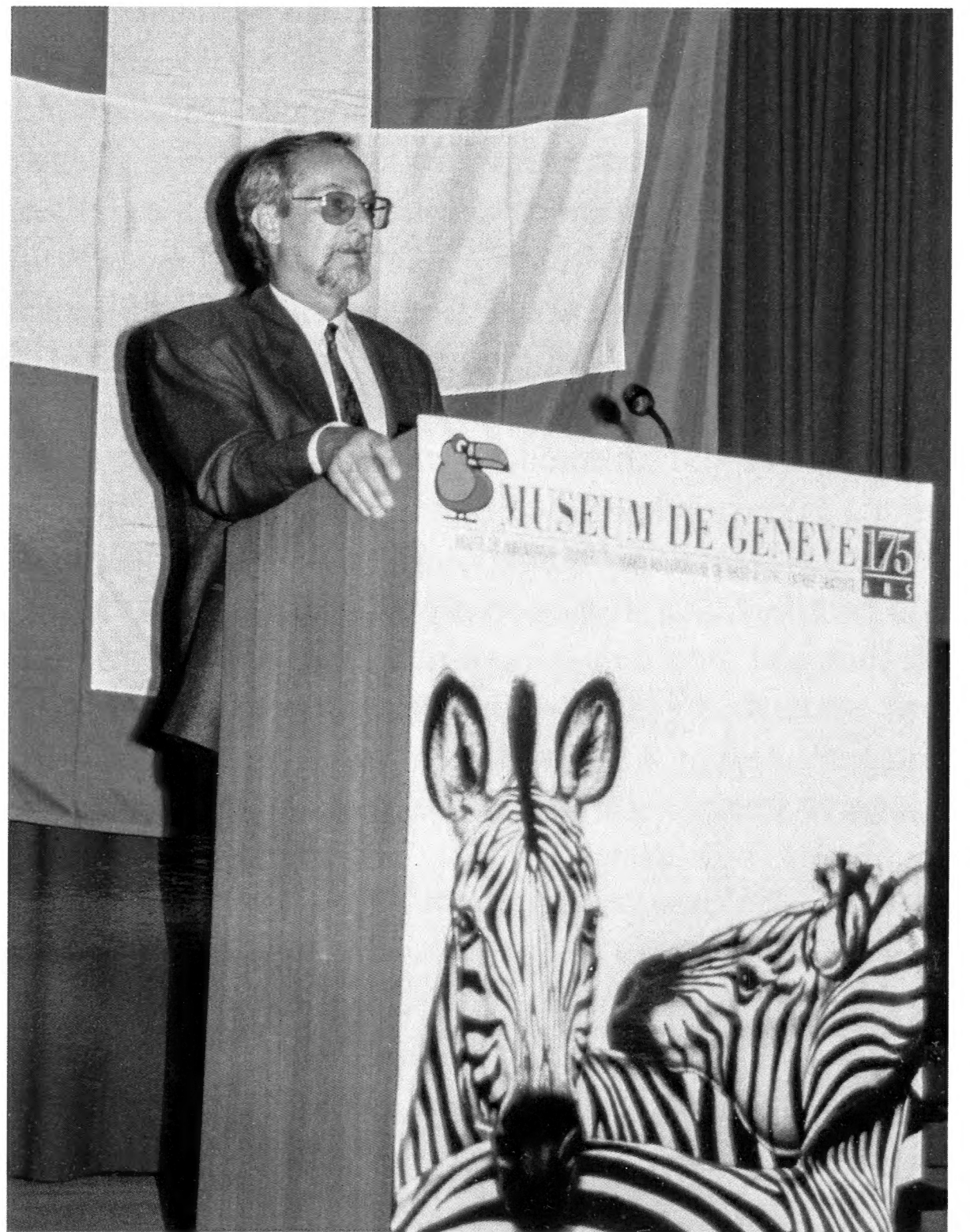
In 1989 Volker Mahnert became director of the museum, again succeeding Villy Aellen, and stayed in office until his retirement in December 2005. He followed the tradition of his predecessors and also became professor of zoology and animal behaviour at the University of Geneva in 1990. He was in the examination committee of numerous students in Innsbruck, Neuchâtel, Geneva, Nancy, Rennes, Paris, São Paulo and Manaus, and he supervised the M. Sc. thesis of 20 students and the Ph. D. thesis of 12 students, three of which (Sonia Fisch-Muller, Raphaël Covain and Lionel Monod) were later employed by the MHNG and one (Juan Montoya-Burgos) by Geneva University.

He pursued this double role (director + professor) until his retirement. Indeed, at that moment he was also interim director of the “Musée d’ethnographie” (from April to December 2005). During all these years he continued to study pseudoscorpions and to publish on them.

Whilst serving as the director of the MHNG from 1989 to 2005, Volker Mahnert was also the editor-in-chief of the *Revue suisse de Zoologie*, and before that (from 1975 to 1989) its co-editor (together with V. Aellen and F. Baud). Between 1997 and 2005 he also edited the *Instrumenta biodiversitatis*, the monograph series of the *Revue suisse de Zoologie*. Additionally he edited the “Catalogue of Pseudoscorpionida to 1988” by Mark S. Harvey

(published by the Manchester University Press in 1990), the “Proceedings of the 13th International Congress of Arachnology, Geneva 3-8 September 1995” (published as a two volume special issue of the *Revue Suisse de Zoologie* in 1996), and he co-edited the series “Fauna of Arabia” between 1996 and 2000.

Volker Mahnert was a member (in some cases a very active one) of several scientific societies and commissions: Federal Scientific Commission for the Surveillance of



Volker Mahnert opening the 13th International Congress of Arachnology, which he organized in the MHNG, on 3 september 1995 (photo C. Ratton, MHNG).



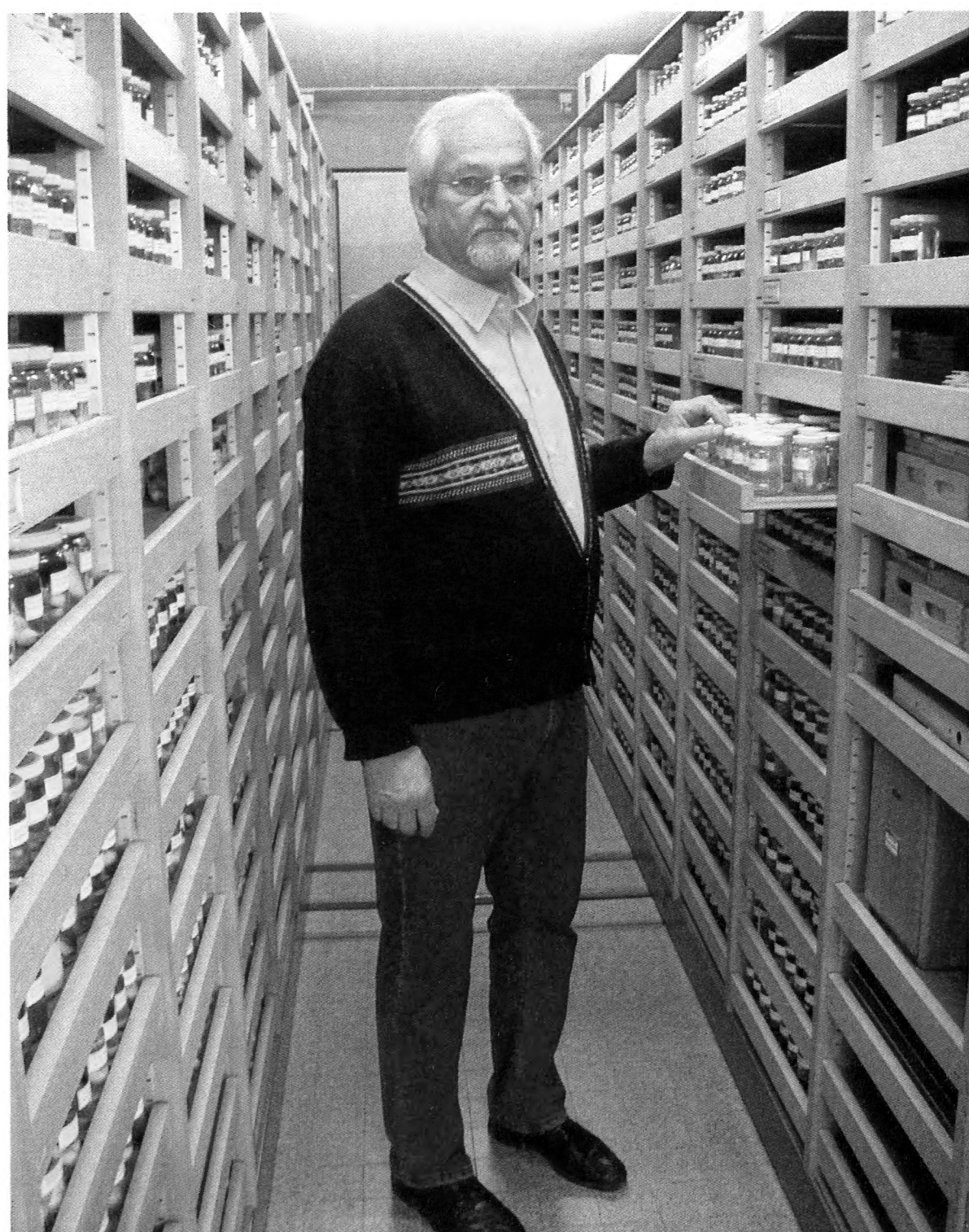
A meeting of Tyrolean zoologists in the MHNG: V. Mahnert, Konrad Thaler (1940-2005; middle) and B. Hauser (right) (photo C. Ratton, MHNG).

Trade in Animals (between 1975 and 1991); Cantonal Commission for the protection of animals; Cantonal Subcommittee for the Surveillance of Keeping and Trading Animals (vice-president between 1981 and 1991); Swiss Zoological Society (vice-president in 1977, central committee member since 1989); Swiss Entomological Society; Arachnologische Gesellschaft (member of the scientific committee of the *Arachnologische Mitteilungen* since its foundation in 1990); French Zoological Society; British arachnological Society; Biological Society of Washington; New York Academy of Sciences; European arachnological Society; European Association of Zoological Nomenclature (president between 1992 and 1996); American arachnological Society; International Society for Subterranean Biology (ISSB); Centre International de Documentation arachnologique (CIDA; president from 1989 to 1992); International Society of Arachnology; International Commission of Zoological Nomenclature (ICZN; commissioner from 1989 to 2007).

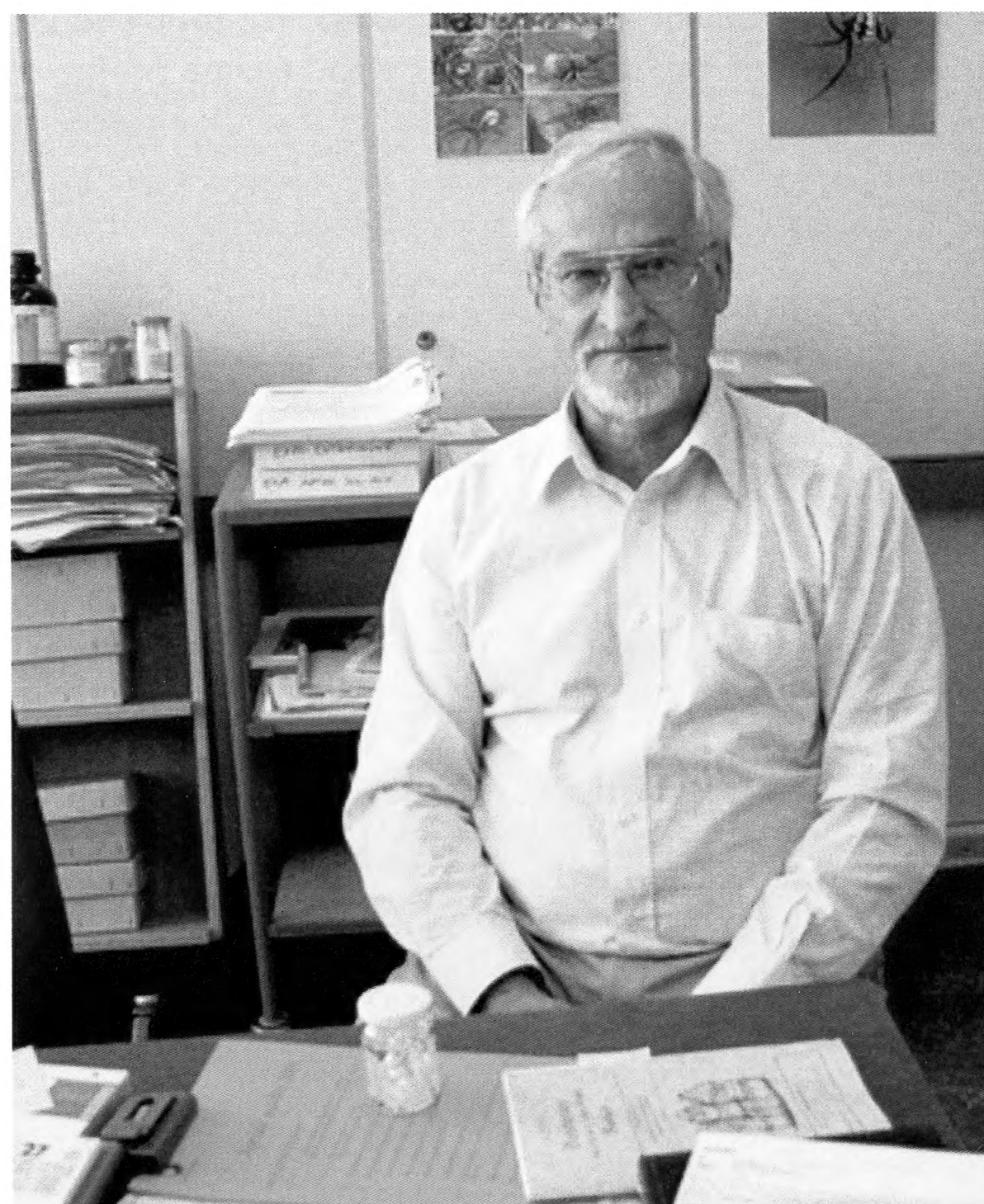
Years before his retirement he and his wife bought a house on the French side of the border, in Douvaine, where he set up a private little “arachnology lab” on the upper floor and continued his studies on pseudoscorpions till the end. He then had the status of honorary director of the MHNG and associate scientist of the Department of Arthropods and Entomology 1. From time to time he came into the museum and brought pseudoscorpion specimens that he

had identified and/or described and that we either placed in the collections of the museum or sent back to other institutions. He only kept a minimum of specimens and literature at home, which made the migration of his lab material to the museum after his death a quite easily manageable undertaking.

Volker Mahnert leaves behind an outstanding scientific legacy: 200 publications (see appendix 1), the descriptions of 20 genera (one genus of fleas, all others pseudoscorpiones) and 350 species/subspecies (6 fleas, 12 fish, all others pseudoscorpions; see appendix 2), and one of the most important pseudoscorpion collections in the world. Originally a fairly modest collection of central European pseudoscorpions composed by Roger de Lessert (1878-1945), V. Mahnert greatly expanded and enriched it with specimens from all over the world and with type specimens through his taxonomic work, through routine identifications and through his extensive scientific network. This excellent collection now contains 1255 nominal species (out of about 3800 species currently known worldwide), 250 of them represented by primary types, plus 87 species that are either new to science or the identity of which is unclear. Apart from this he contributed considerably to the expansion of the fish, mite, lice and flea collections. For the latter his contact with Fritz Peus (1904-1978), whose flea collection is now deposited in the MHNG, was of great importance.



Volker Mahnert in the pseudoscorpion collection of the MHNG (photo P. Schwendinger).



Volker Mahnert in my office, bringing new pseudoscorpions for the MHNG collection (photo P. Schwendinger).

Volker Mahnert was a very gentle person, good-humoured and always with a joke on his lips, never refusing to give advice and information. I never saw him angry and I never met anybody who seriously complained about him. A boss and colleague as one could only wish to have. He was also much liked and respected by fellow scientists in his extensive international network, which is reflected by the fact that there are three animal genera (one genus of pseudoscorpions, the others mites), at least 56 animal species (in the triclads, nematods, tapeworms, earthworms, scorpions, spiders, opilionids, pseudoscorpions, mites, millipedes, diplurans, bugs, beetles, fish, amphibians and snakes) and one mineral named in his honour (see appendix 3). Many more will certainly follow. Volker Mahnert was taken from us in his still productive years – much too early – but his memory will live on far beyond our lifetimes in the scientific results he published and in the scientific collections he amassed.

Appendix 1: List of publications

Parasitology

- Mahnert V. 1970. Über Ento- und Ektoparasiten von Kleinsäugetern der mittleren Ostalpen (Nordtirol). *Ph. D. thesis, University of Innsbruck*, 139 pp.
- Mahnert V. 1970. Trypanosomen aus alpinen Kleinsäugetern Tirols (Österreich). *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck* 58: 131-142.
- Prokopic J., Mahnert V. 1970. Über Helminthen der Kleinsäuger (Insectivora, Rodentia) Tirols (Österreichs). *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck* 58: 143-154.

Arthropoda

- Martius C., Höfer H., Verhaagh M., Adis J., Mahnert V. 1994. Terrestrial arthropods colonizing an abandoned termite nest in a floodplain forest of the Amazon River during the flood. *Andrias* 13: 17-22.
- Adis J., Bonaldo A.B., Brescovit A.D., Bertani R., Cokendolpher J.C., Condé B., Kury A.B., Lourenço W.R., Mahnert V., Pinto-da-Rocha R., Platnick N.I., Reddel J.R., Rheims C.A., Rocher L.S., Rowland J.M., Weygoldt P., Woas S. 2003. Arachnida at “Reserva Ducke”, Central Amazonia / Brazil. *Amazoniana* 17(1/2): 1-14.
- Borges P.A.V., Aguiar L., Amaral J., Amorim I.R., André G., Arraiol A., Baz A., Dinis F., Enghoff H., Gaspar C., Ilharco F., Mahnert V., Melo C., Perlira F., Quartan J.A., Ribeira S.P., Ribes J., Serrano A.R.M., Sousa A.B., Strasser R.Z., Vieira L., Vireia V., Vitorinba A., Wunderlich J. 2005. Ranking protected areas in the Azores using standardised sampling of soil epigeal arthropods. *Biodiversity and Conservation* 14: 2029-2060.
- Baert L., Mahnert V. 2015. The distribution of the non-araneae and non-acari arachnids of Galapagos. *Belgian Journal of Entomology* 28: 1-76.
- Borges P.A.V., Gaspar C., Crespo L., Rigal F., Cardoso P.,

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Anka Mahnert, Danielle Decrouez, Sonia Fisch-Muller, Bernd Hauser, Claude Vaucher and Giulio Gardini provided information on and/or photos of V. Mahnert; Christina Lehmann-Graber compiled information on the pseudoscorpion collection of the MHNG; Raphaël Covain checked for fish types in the MHNG; Philippe Wagneur helped find photos in the MHNG archive and scanned them; Christelle Mouglin clarified some obscure bibliographical references; Mark S. Harvey provided a complete list of pseudoscorpion species described by V. Mahnert; John Hollier checked the English text.

Peter J. Schwendinger
Geneva, 18 February 2019

Pereira F., Rego C., Amorim I.R., Melo C., Aguiar C., André G., Mendonça E., Ribeiro S.P., Hortal J., Santos A.M., Barcelos L., Enghoff H., Mahnert V., Pita M.T., Ribes J., Baz A., Sousa A.B., Vieira V., Wunderlich J., Parmakelis A., Whittaker R.A., Quartan J.A., Serrano A.R.M., Triantis K.A. 2016. New records and detailed distribution and abundance of selected arthropod species collected between 1999 and 2011 in Azorean native forests. *Biodiversity Data Journal* 4: 1-84.

Araneae

- Mahnert V. 1988. Quelle horreur: des araignées sur timbres-poste! *Musées de Genève* 281: 6-12.

Palpigradi

- Mahnert V., Janetschek H. 1970. Bodenlebende Palpenläufer in den Alpen (Arach., Palpigradida). *Oecologia* 4: 106-110.

Pseudoscorpiones

- Mahnert V. 1972. *Neobisium (Blothrur) kwartirnikovi* nov. spec. (Pseudoscorpionidea) aus Bulgarien. *Archives des Sciences* 24: 383-389.
- Mahnert V. 1972. Über griechische Pseudoskorpione I: *Microcreagris leucadia* nov. spec. (Arachnida: Pseudoscorpiones, Neobisiidae). *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck* 59: 51-56.
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- Mahnert V. 1976. Zur Kenntnis der Gattungen *Acanthocreagris* und *Roncocreagris* (Arachnida, Pseudoscorpiones, Neobisiidae). *Revue suisse de Zoologie* 83: 193-214.
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- Mahnert V. 1977. Zwei neue Pseudoskorpion-Arten (Arachnida, Pseudoscorpiones) aus marokkanischen Höhlen. *International Journal of Speleology* 8: 375-381.
- Mahnert V. 1977. Über einige Atemnidae und Cheliferidae Griechenlands (Pseudoscorpiones). *Bulletin de la Société Entomologique Suisse* 50: 67-74.
- Mahnert V. 1977. Etude comparative des trichobothries de pseudoscorpions au microscope électronique à balayage. *Compte rendu des séances de la Société de physique et d'histoire naturelle de Genève* (N. S.) 11: 96-99.
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Appendix 2: Taxa described by Volker Mahnert and depository of corresponding type specimens in MHNG.

* = secondary types present; ** = primary types present; *** = primary and secondary types present

Genera and subgenera:

Acanthocreagris Mahnert, 1974 (Pseudoscorpiones)

Afroroncus Mahnert, 1981 (Pseudoscorpiones)

Alectopsylla Mahnert, 1976 (Siphonaptera)

Attaleachernes Mahnert, 2009 (Pseudoscorpiones)

Beierochelifer Mahnert, 1977 (Pseudoscorpiones)

Beierowithius Mahnert, 1979 (replacement name for *Oligowithius* Beier, 1937; Pseudoscorpiones)

Caecatemnus Mahnert, 1985 (Pseudoscorpiones)

Cardiolphium Mahnert 1986 (Pseudoscorpiones)

Ceratochernes Mahnert, 1994 (Pseudoscorpiones)

Halominniza Mahnert, 1975 (Pseudoscorpiones)

Leptocheiridium Mahnert & Schmidl, 2011 (Pseudoscorpiones)

Microblothrus Mahnert, 1985 (Pseudoscorpiones)

Phymatochernes Mahnert, 1979 (Pseudoscorpiones)

Pseudomenthus Mahnert, 2007 (Pseudoscorpiones)

Roncocreagris Mahnert, 1974 (originally a subgenus of *Microcreagris*; Pseudoscorpiones)

Selachochernes Mahnert, 2001 (Pseudoscorpiones)

Spelaeobochica Mahnert, 2001 (Pseudoscorpiones)

Spelaeochernes Mahnert, 2001 (Pseudoscorpiones)

Sphaerowithius Mahnert, 1988 (Pseudoscorpiones)

Xorilbia Harvey & Mahnert, 2006 (Pseudoscorpiones)

Acanthocreagris relictata Mahnert, 1977 (Pseudoscorpiones) *

Acanthocreagris vachoni Mahnert, 1976 [currently in the synonymy of *Acanthocreagris ronciformis* (Redikorzev, 1949); Pseudoscorpiones] ***

Afrogarypus quadrimaculatus Mahnert, 2007 (Pseudoscorpiones) ***

Afroroncus kikuyu Mahnert, 1981 (Pseudoscorpiones)***

Afroroncus sulcatus Mahnert, 1981 (Pseudoscorpiones)*

Albiorix lamellifer Mahnert, 1985 (Pseudoscorpiones)

Albiorix gracilis Mahnert, 1985 (currently in *Xorilbia*; Pseudoscorpiones)***

Alectopsylla unisetosa Mahnert, 1976 (Siphonaptera)***

Allochernes longepilosus Mahnert, 1997 (Pseudoscorpiones)***

Allochernes maroccanus Mahnert, 1976 (Pseudoscorpiones)***

Allochernes peregrinans Mahnert, 2009 (Pseudoscorpiones)**

Amblyolpium graecum Mahnert, 1976 (Pseudoscorpiones)**

Americhernes bethaniae Mahnert, 1979 (Pseudoscorpiones)*

Americhernes incertus Mahnert, 1979 (Pseudoscorpiones)*

Anaperochernes margaritifera Mahnert, 1985 (Pseudoscorpiones)

Apocheiridium cavicola Mahnert, 1993 (Pseudoscorpiones)**

Apocheiridium lienhardi Mahnert, 2011 (Pseudoscorpiones)***

Apocheiridium pallidum Mahnert, 1982 (Pseudoscorpiones)***

Apolpiolum gigas Mahnert, 1980 (currently in *Calocheirus*; Pseudoscorpiones)

Attaleachernes thaleri Mahnert, 2009 (Pseudoscorpiones)*

Barbus condei Mahnert & Géry, 1982 (currently in *Enteromius*; Pisces)***

Barbus prionacanthus Mahnert & Géry, 1982 (currently in *Enteromius*; Pisces)

Beierolpium benoitii Mahnert, 1978 (Pseudoscorpiones)*

Beierolpium flavum Mahnert, 1984 (Pseudoscorpiones)*

Beierolpium holmi Mahnert, 1982 (Pseudoscorpiones)*

Species and subspecies:

Acanthocreagris aelleni Mahnert, 1978 (Pseudoscorpiones) **

Acanthocreagris beieri Mahnert, 1974 (Pseudoscorpiones) **

Acanthocreagris corcyraea Mahnert, 1976 (Pseudoscorpiones) **

Acanthocreagris corsa Mahnert, 1974 (Pseudoscorpiones) ***

Acanthocreagris leucadia epirensis Mahnert, 1974 (Pseudoscorpiones) ***

Acanthocreagris lycaonis Mahnert, 1978 (Pseudoscorpiones) ***

Acanthocreagris obtusa Mahnert, 1976 (Pseudoscorpiones) ***

- Beierolpium kerioense* Mahnert, 1982 (Pseudoscorpiones)***
Beierolpium tanense Mahnert, 1982 (Pseudoscorpiones)***
Beierolpium vanharteni Mahnert, 2007 (Pseudoscorpiones)***
Bisetocreagris baozinensis Mahnert & Li, 2016
(Pseudoscorpiones)*
Bisetocreagris cavernarum Mahnert & Li, 2016
(Pseudoscorpiones)*
Bisetocreagris chuanensis Mahnert & Li, 2016
(Pseudoscorpiones)*
Bisetocreagris juanxuae Mahnert & Li, 2016
(Pseudoscorpiones)*
Brycinus derhami Géry & Mahnert, 1977 (Pisces)***
Brycinus longipinnis bagbeensis Géry & Mahnert, 1977
[currently in the synonymy of *Bryconalestes longipinnis* (Günther, 1864); Pisces]
Caecatemnus setosipygus Mahnert, 1985 (Pseudoscorpiones)*
Caffrowithius biseriatatus Mahnert, 1983 (Pseudoscorpiones)*
Caffrowithius planicola Mahnert, 1982 (Pseudoscorpiones)***
Calocheiridius gracilipalpus Mahnert, 1982
(Pseudoscorpiones)***
Calocheirus gracilis Mahnert, 1991 (Pseudoscorpiones)*
Calocheirus mirus Mahnert, 1986 (Pseudoscorpiones)***
Calocheirus tenerifae Mahnert 2002 (Pseudoscorpiones)
Catatemnus exiguus Mahnert, 1978 (Pseudoscorpiones)***
Catatemnus granulatus Mahnert, 1978 (Pseudoscorpiones)
Ceratochernes granulatus Mahnert, 1994 (Pseudoscorpiones)*
Ceratochernes guanophilus Mahnert, 1994
(Pseudoscorpiones)*
Ceriochernes amazonicus Mahnert, 1985 (Pseudoscorpiones)*
Cheiridium brasiliense Mahnert, 2001 (Pseudoscorpiones)*
Cheiridium perreti Mahnert, 1982 (Pseudoscorpiones)***
Cheiridium somalicum Mahnert, 1984 (Pseudoscorpiones)*
Cheiridium tumidum Mahnert 1982 (Pseudoscorpiones)***
Chelanops gracilipalpus Mahnert, 2011
(Pseudoscorpiones)***
Chelanops gracilipes Mahnert, 2011 (Pseudoscorpiones)**
Chelanops (Neochelanops) peruanus Mahnert, 1984 (currently
in genus *Neochelanops*; Pseudoscorpiones)*
Chthonius (Chthonius) apollinis Mahnert, 1978
(Pseudoscorpiones)***
Chthonius (Chthonius) herbarii Mahnert, 1980
(Pseudoscorpiones)***
Chthonius (Chthonius) hungaricus Mahnert, 1981
(Pseudoscorpiones)*
Chthonius (Chthonius) imperator Mahnert, 1978
(Pseudoscorpiones)***
Chthonius (Chthonius) lucifugus Mahnert, 1977
(Pseudoscorpiones)
Chthonius (Chthonius) ponticoides Mahnert, 1975
(Pseudoscorpiones)**
Chthonius (Chthonius) sestasi Mahnert 1980
(Pseudoscorpiones)***
Chthonius (Chthonius) strinatii Mahnert, 1975
(Pseudoscorpiones)***
Chthonius (Chthonius) thessalus Mahnert, 1980
(Pseudoscorpiones)***
Chthonius (Chthonius) tzanoudakisi Mahnert, 1975
(Pseudoscorpiones)***
Chthonius (Ephippiochthonius) atlantis Mahnert,
1980 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)**
Chthonius (Ephippiochthonius) balearicus Mahnert,
1977 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)*
Chthonius (Ephippiochthonius) bellesi Mahnert,
1989 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)*
Chthonius (Ephippiochthonius) cabrieriensis Mahnert,
1993 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)
Chthonius (Ephippiochthonius) corcyraeus Mahnert,
1976 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)**
Chthonius (Ephippiochthonius) creticus Mahnert,
1980 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)***
Chthonius (Ephippiochthonius) daedaleus Mahnert,
1980 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)***
Chthonius (Ephippiochthonius) dubius Mahnert, 1993
(currently in *Occidenchthonius*; Pseudoscorpiones)**
Chthonius (Ephippiochthonius) girgentiensis Mahnert,
1982 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)**
Chthonius (Ephippiochthonius) gracilimanus Mahnert, 1997
(currently in *Occidenchthonius*; Pseudoscorpiones)*
Chthonius (Ephippiochthonius) longesetosus Mahnert,
1976 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)**
Chthonius (Ephippiochthonius) lopezi Mahnert, 2011
(currently in *Occidenchthonius*; Pseudoscorpiones)*
Chthonius (Ephippiochthonius) maltensis Mahnert,
1975 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)*
Chthonius (Ephippiochthonius) maroccanus Mahnert,
1980 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)**
Chthonius (Ephippiochthonius) minous minous Mahnert,
1980 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)***
Chthonius (Ephippiochthonius) minous peramaea Mahnert,
1980 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)*
Chthonius (Ephippiochthonius) nidicola Mahnert,
1979 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)***
Chthonius (Ephippiochthonius) nudipes Mahnert,
1982 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)*
Chthonius (Ephippiochthonius) platakisi Mahnert,
1980 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)***
Chthonius (Ephippiochthonius) poeninus Mahnert 1979
(currently in *Globochthonius*; Pseudoscorpiones)***
Chthonius (Ephippiochthonius) ponsi Mahnert,
1993 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)*
Chthonius (Ephippiochthonius) rimicola Mahnert,
1993 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)*
Chthonius (Ephippiochthonius) samius Mahnert,
1982 (currently in genus *Ephippiochthonius*;
Pseudoscorpiones)***
Chthonius (Ephippiochthonius) setosus Mahnert, 1993
(currently in *Occidenchthonius*; Pseudoscorpiones)**
Chthonius (Ephippiochthonius) tamaran Mahnert, 2011
(currently in *Occidenchthonius*; Pseudoscorpiones)*

- Chthonius (Ephippiochthonius) tenerifae* Mahnert, 2011
(currently in *Occidenchthonius*; Pseudoscorpiones)
- Creagrutus paraguayensis* Mahnert & Géry, 1988 (Pisces)***
- Creagrutus pearsoni* Mahnert & Géry, 1988 (Pisces)
- Cryptocheiridium confundens* Mahnert, 2014
(Pseudoscorpiones)*
- Ctenophthalmus (Ethioctenophthalmus) digitosignatus*
Mahnert, 1977 (Siphonaptera) ***
- Cyclatennus brevidigitatus* Mahnert, 1978 (Pseudoscorpiones)
- Dactylochelifer arabicus* Mahnert, 1991 (Pseudoscorpiones)*
- Dactylochelifer besucheti* Mahnert, 1978
(Pseudoscorpiones)***
- Dactylochelifer scaurus* Mahnert, 1978 (Pseudoscorpiones)**
- Dactylochelifer vtorovi* Mahnert, 1977 (Pseudoscorpiones)***
- Dasychnes panamensis* Mahnert, 1987
(Pseudoscorpiones)***
- Dasychnes roubiki* Mahnert, 1987 (Pseudoscorpiones)***
- Dasychnes trigonae* Mahnert, 1987 (Pseudoscorpiones)***
- Dhanus pohli* Mahnert, 2007 (currently in *Shravana*;
Pseudoscorpiones)
- Dhanus socotraensis* Mahnert, 2007 (currently in *Shravana*;
Pseudoscorpiones)***
- Dhanus taitii* Mahnert, 2007 (currently in *Shravana*;
Pseudoscorpiones)*
- Dolichowithius (Dolichowithius) intermedius* Mahnert, 1979
(Pseudoscorpiones)*
- Dolichowithius (Dolichowithius) mediofasciatus* Mahnert,
1979 (Pseudoscorpiones)*
- Dolichowithius (Dolichowithius) minutus* Mahnert, 1979
(Pseudoscorpiones)*
- Elattogarypus cicatricosus* Mahnert, 2007
(Pseudoscorpiones)*
- Elattogarypus somalicus* Mahnert 1984 (Pseudoscorpiones)*
- Feaella (Tetrafeaella) perreti* Mahnert, 1982
(Pseudoscorpiones)***
- Garypus darsahensis* Mahnert, 2007 (Pseudoscorpiones)
- Garypinus nicolaii* Mahnert, 1988 (Pseudoscorpiones)*
- Garypus granosus* Mahnert, 2014 (Pseudoscorpiones)*
- Garypus marmoratus* Mahnert, 1982 (Pseudoscorpiones)***
- Garypus occultus* Mahnert, 1982 (Pseudoscorpiones)***
- Geogarypus (Afrogarypus) plumatus* Mahnert, 1982 (currently
in *Afrogarypus*; Pseudoscorpiones)***
- Geogarypus (Afrogarypus) pseudocurtus* Mahnert, 1982
(currently in *Afrogarypus*; Pseudoscorpiones)***
- Geogarypus (Afrogarypus) stellifer* Mahnert, 1982 (currently
in *Afrogarypus*; Pseudoscorpiones)***
- Geogarypus (Geogarypus) amazonicus* Mahnert, 1979
(Pseudoscorpiones)*
- Geogarypus (Geogarypus) ocellatus* Mahnert, 1978
(Pseudoscorpiones)*
- Geogarypus quadrimaculatus* Mahnert, 2007
(Pseudoscorpiones)
- Halominniza oromii* Mahnert, 1997 (Pseudoscorpiones)
- Halominniza parentorum* Mahnert, 1975
(Pseudoscorpiones)**
- Halominniza taitii* Mahnert, 2007 (Pseudoscorpiones)
- Haplochernes nanus* Mahnert, 1975 (Pseudoscorpiones)***
- Hectopsylla gracilis* Mahnert, 1982 (Siphonaptera)***
- Hemigrammus bleheri* Géry & Mahnert, 1986 (Pisces)*
- Hyphessobrycon guarani* Mahnert & Géry, 1987 (currently in
Diapoma; Pisces)***
- Hyphessobrycon procerus* Mahnert & Géry, 1987 (Pisces)***
- Hyphessobrycon pytai* Mahnert & Géry, 1993 (Pisces)***
- Ideobisium schusteri* Mahnert, 1985 (Pseudoscorpiones)***
- Ideobisium amazonicum* Mahnert, 1979 (currently in
Ideoblothrus; Pseudoscorpiones)*
- Ideobisium baloghi* Mahnert, 1978 (currently in *Ideoblothrus*;
Pseudoscorpiones)*
- Ideobisium brasiliense* Mahnert, 1979 (currently in
Ideoblothrus; Pseudoscorpiones)*
- Ideobisium caecum* Mahnert, 1979 (currently in *Ideoblothrus*;
Pseudoscorpiones)*
- Ideobisium zicsii* Mahnert, 1978 (currently in *Ideoblothrus*;
Pseudoscorpiones)*
- Ideoblothrus emigrans* Mahnert, 2014 (Pseudoscorpiones)*
- Ideoblothrus galapagensis* Mahnert, 2014
(Pseudoscorpiones)***
- Ideoblothrus levipalpus* Mahnert, 1985 (Pseudoscorpiones)**
- Ideoblothrus paraensis* Mahnert, 1985 (Pseudoscorpiones)*
- Ideoblothrus tenuis* Mahnert, 1985 (Pseudoscorpiones)*
- Ideoroncus anophthalmus* Mahnert, 1984
(Pseudoscorpiones)***
- Ideoroncus arboricola* Mahnert, 1979 (currently in *Xorilbia*;
Pseudoscorpiones)*
- Ideoroncus beieri* Mahnert, 1984 (Pseudoscorpiones)***
- Ideoroncus cavicola* Mahnert, 2001 (Pseudoscorpiones)*
- Ideoroncus divisus* Mahnert, 1984 (Pseudoscorpiones)*
- Ideoroncus paranensis* Mahnert, 1984 (Pseudoscorpiones)***
- Ideoroncus setosus* Mahnert, 1984 (Pseudoscorpiones)***
- Lagynochthonius curvidigitatus* Mahnert, 1997
(Pseudoscorpiones)
- Lagynochthonius insulanus* Mahnert, 2007
(Pseudoscorpiones)***
- Lagynochthonius lopezi* Mahnert, 2011 (Pseudoscorpiones)*
- Lagynochthonius microdentatus* Mahnert, 2011
(Pseudoscorpiones)
- Lagynochthonius oromii* Mahnert, 2011 (Pseudoscorpiones)*
- Lagynochthonius subterraneus* Mahnert, 2011
(Pseudoscorpiones)*
- Lagynochthonius tenuimanus* Mahnert, 2011
(Pseudoscorpiones)*
- Lechytia dentata* Mahnert, 1978 (Pseudoscorpiones)
- Leporinus falcipinnis* Mahnert, Géry & Muller, 1997
(currently in the synonymy of *Leporinus altipinnis*
Borodin, 1929; Pisces)
- Leptocheiridium pfeifferae* Mahnert & Schmidl, 2011
(Pseudoscorpiones)***
- Levigatocreagris hamatus* Leclerc & Mahnert, 1988 (currently
in *Stenoya*; Pseudoscorpiones)***
- Lophochelifer gracilipes* Mahnert, 1988 (currently in
Lissochelifer; Pseudoscorpiones)***
- Lophochelifer nairobiensis* Mahnert, 1988 (currently in
Lissochelifer; Pseudoscorpiones)***
- Maxchnes iporangae* Mahnert & Andrade, 1998
(Pseudoscorpiones)*
- Megachernes glandulosus* Mahnert, 2009
(Pseudoscorpiones)**
- Megachernes tuberosus* Mahnert, 2009 (Pseudoscorpiones)***
- Mesochelifer resli* Mahnert, 1981 (Pseudoscorpiones)***
- Metastivalius novaehiberniae* Beaucournu & Mahnert, 1988
(Siphonaptera)***
- Micratennus crassipes* Mahnert, 1983 (Pseudoscorpiones)***
- Microblothrus trident* Mahnert, 1985 (Pseudoscorpiones)*
- Microchelifer dentatus* Mahnert, 1988 (Pseudoscorpiones)**
- Microcreagrina cavicola* Mahnert, 1993 (Pseudoscorpiones)*
- Microcreagrina gomeræ* Mahnert, 1993 [currently in the
synonymy of *Microcreagrina hispanica* (Ellingsen,
1910); Pseudoscorpiones]**

- Microcreagrina madeirensis* Mahnert, 1993
(Pseudoscorpiones)**
- Microcreagrina subterranea* Mahnert, 1993
(Pseudoscorpiones)*
- Microcreagris leucadia* Mahnert, 1972 [currently in
Acanthocreagris; Pseudoscorpiones]**
- Minniza antonii* Mahnert, 2009 (Pseudoscorpiones)***
- Minniza barkhamae* Mahnert, 1991 (Pseudoscorpiones)*
- Minniza elegans* Mahnert, 1991 (Pseudoscorpiones)*
- Minniza gallagheri* Mahnert, 1991 (Pseudoscorpiones)*
- Minniza levisetosa* Mahnert, 1991 (Pseudoscorpiones)*
- Minniza monticola* Mahnert, 1991 (Pseudoscorpiones)*
- Minniza nigrimanus* Mahnert, 1991 (Pseudoscorpiones)*
- Miratemnus kenyaensis* Mahnert, 1983 (Pseudoscorpiones)***
- Myrmecowithius buettikeri* Mahnert, 1980 (currently in
Nannowithius; Pseudoscorpiones)*
- Myrmecowithius paradoxus* Mahnert, 1980 now in
Nannowithius; Pseudoscorpiones)*
- Nannobisium beieri* Mahnert, 1979 (Pseudoscorpiones)*
- Negroroncus azanius* Mahnert, 1981 (Pseudoscorpiones)***
- Negroroncus densedentatus* Mahnert, 1981
(Pseudoscorpiones)
- Negroroncus gregoryi* Mahnert, 1981 (Pseudoscorpiones)***
- Negroroncus kerenyaga* Mahnert, 1981 (Pseudoscorpiones)**
- Negroroncus silvicola* Mahnert, 1981 (Pseudoscorpiones)*
- Negroroncus tsavoensis* Mahnert, 1981 (Pseudoscorpiones)***
- Neobisium (Blothrus) cervelloi* Mahnert, 1977
(Pseudoscorpiones)
- Neobisium (Blothrus) hians* Mahnert, 1979 (Pseudoscorpiones)
- Neobisium (Blothrus) kwartirnikovi* Mahnert, 1972
(Pseudoscorpiones)***
- Neobisium (Blothrus) monasterii* Mahnert, 1977
(Pseudoscorpiones)*
- Neobisium (Neobisium) bosnicum ondriasi* Mahnert, 1973
(Pseudoscorpiones)***
- Neobisium (Neobisium) intermedium* Mahnert, 1974
(Pseudoscorpiones)***
- Neobisium (Neobisium) phitosi* Mahnert, 1973
(Pseudoscorpiones)***
- Neobisium (Neobisium) reductum* Mahnert, 1977
(Pseudoscorpiones)*
- Neobisium (Ommatoblothrus) gaditanum* Mahnert, 1977
(Pseudoscorpiones)
- Neobisium (Ommatoblothrus) patrizii romanum* Mahnert,
1980 (Pseudoscorpiones)
- Neobisium (Ommatoblothrus) paucedentatum* Mahnert, 1982
(Pseudoscorpiones)*
- Neobisium (Ommatoblothrus) phaeacum* Mahnert, 1973
(Pseudoscorpiones)***
- Neobisium (Ommatoblothrus) samniticum* Mahnert, 1980
(Pseudoscorpiones)*
- Neocheiridium africanum* Mahnert, 1982 (Pseudoscorpiones)*
- Neocheiridium pusillum* Mahnert, 1982
(Pseudoscorpiones)***
- Neocheiridium strinatii* Mahnert & Aguiar, 1986
(Pseudoscorpiones)***
- Neocheiridium triangulare* Mahnert & Aguiar, 1986
(Pseudoscorpiones)*
- Nesowithius dilatimanus* Mahnert, 1988
(Pseudoscorpiones)***
- Nhatrangia ceylonensis* Mahnert, 1984 (currently in *Shravana*;
Pseudoscorpiones)***
- Nudochernes gracilimanus* Mahnert, 1982
(Pseudoscorpiones)***
- Nudochernes lipsae* Mahnert, 2003 (Pseudoscorpiones)**
- Nudochernes troglobius* Mahnert, 2009
(Pseudoscorpiones)***
- Olpium flavum* Mahnert, 2007 (Pseudoscorpiones)***
- Olpium halophilum* Mahnert, 1982 (Pseudoscorpiones)***
- Olpium kuriense* Mahnert, 2007 (Pseudoscorpiones)*
- Olpium milneri* Mahnert, 2007 (Pseudoscorpiones)***
- Olpium omanense* Mahnert, 1991 (Pseudoscorpiones)
- Olpium socotraense* Mahnert, 2007 (Pseudoscorpiones)***
- Olpium vanharteni* Mahnert, 2007 (Pseudoscorpiones)***
- Pachyolpium atlanticum* Mahnert & Schuster, 1981
(Pseudoscorpiones)***
- Pachyolpium irmgardae* Mahnert, 1979 (Pseudoscorpiones)*
- Parachernes adisi* Mahnert, 1979 (Pseudoscorpiones)*
- Parachernes gracilimanus* Mahnert, 1986
(Pseudoscorpiones)***
- Parachernes inpai* Mahnert, 1979 (Pseudoscorpiones)*
- Parachernes niger* Mahnert 1987 (Pseudoscorpiones)*
- Parachernes ovatus* Mahnert, 1979 (Pseudoscorpiones)*
- Parachernes pulcher* Mahnert, 1979 (Pseudoscorpiones)
- Parachernes setiger* Mahnert, 1979 (Pseudoscorpiones)*
- Paraliochthonius azanius* Mahnert, 1986
(Pseudoscorpiones)***
- Paraliochthonius galapagensis* Mahnert, 2014
(Pseudoscorpiones)***
- Paraliochthonius litoralis* Mahnert, 2014 (Pseudoscorpiones)*
- Paraliochthonius martini* Mahnert, 1989 (Pseudoscorpiones)*
- Paraliochthonius mirus* Mahnert, 2002 (Pseudoscorpiones)*
- Paraliochthonius pecki* Mahnert, 2014 (Pseudoscorpiones)***
- Paraliochthonius rupicola* Mahnert, 2014
(Pseudoscorpiones)***
- Paraliochthonius tenebrarum* Mahnert, 1989
(Pseudoscorpiones)
- Paramenthus nanus* Mahnert, 2007 (Pseudoscorpiones)*
- Parawithius (Victorwithius) coniger* Mahnert, 1979 (currently
in *Victorwithius*; Pseudoscorpiones)*
- Parawithius (Victorwithius) gracilimanus* Mahnert, 1979
(currently in *Victorwithius*; Pseudoscorpiones)*
- Parobisium martii* Mahnert, 2003 (currently in *Bisetocreagris*;
Pseudoscorpiones)**
- Parobisium scaurum* Mahnert, 2003 (currently in
Bisetocreagris; Pseudoscorpiones)**
- Parobisium titanium* Mahnert, 2003 (currently in
Bisetocreagris; Pseudoscorpiones)**
- Petterchernes tuberculatus* Mahnert, 1994
(Pseudoscorpiones)*
- Phymatochernes crassimanus* Mahnert, 1979
(Pseudoscorpiones)
- Piabarchus torrenticola* Mahnert & Géry, 1988 (Pisces)***
- Pilochelifer insularis gracilior* Mahnert, 1975
(Pseudoscorpiones)***
- Plesiochernes bergeri* Mahnert, 1978 (currently in
Caffrowithius; Pseudoscorpiones)**
- Plocopsylla angusticeps* Mahnert, 1982 (Siphonaptera)**
- Progarypus gracilis* Mahnert, 2001 (Pseudoscorpiones)*
- Progarypus liliae* Mahnert, 2001 (Pseudoscorpiones)
- Progarypus nigrimanus* Mahnert, 2001 (Pseudoscorpiones)*
- Progarypus setifer* Mahnert, 2001 (Pseudoscorpiones)*
- Pseudoblothrus infernus* Mahnert, 2011 (Pseudoscorpiones)**
- Pseudoblothrus oromii* Mahnert, 1990 (Pseudoscorpiones)*
- Pseudoblothrus vulcanus* Mahnert 1990 (Pseudoscorpiones)*
- Pseudochernes arabicus* Mahnert, 1991 (Pseudoscorpiones)
- Pseudochiridium kenyense* Mahnert, 1982
(Pseudoscorpiones)*

Pseudochthonius arabicus Mahnert, 2014
(Pseudoscorpiones)**

Pseudochthonius beieri Mahnert, 1978 (Pseudoscorpiones)*

Pseudochthonius biseriatus Mahnert, 2001
(Pseudoscorpiones)*

Pseudochthonius gracilimanus Mahnert, 2001
(Pseudoscorpiones)*

Pseudochthonius perreti Mahnert, 1986 (Pseudoscorpiones)*

Pseudochthonius ricardoi Mahnert, 2001 (Pseudoscorpiones)

Pseudochthonius tuxeni Mahnert, 1979 (Pseudoscorpiones)*

Pseudohorus embuensis Mahnert, 1982
(Pseudoscorpiones)***

Pseudohorus luscus Mahnert, 1982 (Pseudoscorpiones)***

Pseudohorus pilosus Mahnert, 1982 (Pseudoscorpiones)***

Pseudohorus vermis Mahnert, 1982 (Pseudoscorpiones)***

Pseudomenthus spinifer Mahnert, 2007 (Pseudoscorpiones)*

Pseudomenthus uniseriatus Mahnert, 2007
(Pseudoscorpiones)**

Pseudopilanus crassifemoratus Mahnert, 1985
(Pseudoscorpiones)*

Pseudorhacochelifer canariensis Mahnert, 1997
(Pseudoscorpiones)*

Pycnowithius cavernicola Mahnert, 1988
(Pseudoscorpiones)***

Rhacochelifer barkhamae Mahnert, 1980 (Pseudoscorpiones)

Rhacochelifer corcyrensis procerus Mahnert, 1978
(Pseudoscorpiones)***

Rhacochelifer euboicus Mahnert, 1977 (Pseudoscorpiones)**

Rhacochelifer gracilimanus Mahnert, 1993
(Pseudoscorpiones)***

Rhacochelifer sonyae Mahnert, 1991 (Pseudoscorpiones)*

Rhacochelifer spiniger Mahnert, 1978 (currently in
Pseudorhacochelifer; Pseudoscorpiones)*

Roncocreagris beieri Mahnert, 1976 (Pseudoscorpiones)***

Roncus gasparoi Mahnert & Gardini, 2014
(Pseudoscorpiones)**

Roncus giachinoi Mahnert & Gardini, 2014
(Pseudoscorpiones)***

Roncus pieperi Mahnert & Gardini, 2014
(Pseudoscorpiones)***

Roncus (Parablothrus) boneti tarbenae Mahnert, 1977
(Pseudoscorpiones)*

Roncus (Parablothrus) comasi Mahnert, 1985
(Pseudoscorpiones)*

Roncus (Parablothrus) corcyraeus minor Mahnert, 1975
(Pseudoscorpiones)***

Roncus (Parablothrus) paolettii Mahnert, 1980
(Pseudoscorpiones)*

Roncus (Parablothrus) puddui Mahnert, 1976
(Pseudoscorpiones)***

Roncus (Roncus) giganteus Mahnert, 1973
(Pseudoscorpiones)***

Roncus (Roncus) viti Mahnert, 1974 (Pseudoscorpiones)**

Selachochernes allodentatus Mahnert, 2001
(Pseudoscorpiones)**

Serianus elongatus Mahnert 2014 (Pseudoscorpiones)***

Serianus maritimus Mahnert 2014 (Pseudoscorpiones)***

Serianus sahariensis Mahnert, 1988 (Pseudoscorpiones)***

Spelaeobochica allodentatus Mahnert, 2001
(Pseudoscorpiones)*

Spelaeobochica iuii Ratton, Mahnert & Ferreira, 2012
(Pseudoscorpiones)*

Spelaeobochica muchmorei Andrade & Mahnert, 2003
(Pseudoscorpiones)*

Spelaeochernes altamirae Mahnert, 2001 (Pseudoscorpiones)*

Spelaeochernes armatus Mahnert, 2001 (Pseudoscorpiones)*

Spelaeochernes bahiensis Mahnert, 2001 (Pseudoscorpiones)*

Spelaeochernes dentatus Mahnert, 2001 (Pseudoscorpiones)*

Spelaeochernes dubius Mahnert, 2001 (Pseudoscorpiones)*

Spelaeochernes eleonora Mahnert, 2001 (Pseudoscorpiones)*

Spelaeochernes gracilipalpus Mahnert, 2001
(Pseudoscorpiones)*

Spelaeochernes pedroi Mahnert, 2001 (Pseudoscorpiones)*

Sphaerowithius ansieae Harvey & Mahnert, 2015
(Pseudoscorpiones)***

Stenolpium fasciculatum Mahnert, 1984 (Pseudoscorpiones)

Thaumastogarypus mancus Mahnert, 1982
(Pseudoscorpiones)**

Thaumatoewithius aberrans Mahnert, 1975
(Pseudoscorpiones)***

Titanatemnus tanensis Mahnert, 1983 (Pseudoscorpiones)***

Tridenchthonius beieri Mahnert, 1983 (Pseudoscorpiones)***

Tridenchthonius brasiliensis Mahnert, 1979
(Pseudoscorpiones)*

Typhloceras poppei orientalis Mahnert & Beaucournu, 1985
(Siphonaptera)**

Tyrannochthonius akaleus Mahnert, 2009
(Pseudoscorpiones)**

Tyrannochthonius (Tyrannochthonius) amazonicus Mahnert,
1979 (Pseudoscorpiones)*

Tyrannochthonius antridraconis Mahnert, 2009
(Pseudoscorpiones)***

Tyrannochthonius (Tyrannochthonius) brasiliensis Mahnert,
1979 (Pseudoscorpiones)

Tyrannochthonius confusus Mahnert, 1986
(Pseudoscorpiones)*

Tyrannochthonius ferox Mahnert, 1978 (currently in
Lagynochthonius; Pseudoscorpiones)

Tyrannochthonius (Lagynochthonius?) flavus Mahnert, 1986
(currently in *Lagynochthonius*; Pseudoscorpiones)***

Tyrannochthonius ganshuanensis Mahnert, 2009
(Pseudoscorpiones)***

Tyrannochthonius (Tyrannochthonius) gomyi Mahnert, 1975
(Pseudoscorpiones)**

Tyrannochthonius (Lagynochthonius) guasirih Mahnert, 1988
(currently in *Lagynochthonius*; Pseudoscorpiones)***

Tyrannochthonius (Tyrannochthonius) irmieri Mahnert, 1979
(currently in *Lagynochthonius*; Pseudoscorpiones)*

Tyrannochthonius (Lagynochthonius?) kenyensis
Mahnert, 1986 (currently in *Lagynochthonius*;
Pseudoscorpiones)***

Tyrannochthonius mahunkai Mahnert, 1978
(Pseudoscorpiones)*

Tyrannochthonius (Tyrannochthonius) migrans Mahnert, 1979
(Pseudoscorpiones)*

Tyrannochthonius (Tyrannochthonius) minor Mahnert, 1979
(currently in *Lagynochthonius*; Pseudoscorpiones)*

Tyrannochthonius procerus Mahnert, 1978
(Pseudoscorpiones)*

Tyrannochthonius pugnax Mahnert, 1978 (currently in
Lagynochthonius; Pseudoscorpiones)*

Tyrannochthonius riberai Mahnert, 1984 (Pseudoscorpiones)*

Tyrannochthonius (Tyrannochthonius) rotundimanus Mahnert,
1985 (Pseudoscorpiones)*

Tyrannochthonius setiger Mahnert, 1997 (currently in
Paraliochthonius; Pseudoscorpiones)*

Tyrannochthonius (Tyrannochthonius) simulans Mahnert,
1986 (Pseudoscorpiones)***

Tyrannochthonius (Tyrannochthonius) superstes
Mahnert, 1986 (currently in *Paraliochthonius*;
Pseudoscorpiones)*
Tyrannochthonius zicsii Mahnert, 1978 (currently in
Lagynochthonius; Pseudoscorpiones)
Withius (Allowithius) arabicus Mahnert, 1980
(Pseudoscorpiones)*

Withius brevidigitatus Mahnert, 1988 (Pseudoscorpiones)***
Withius fuscus Mahnert, 1988 (Pseudoscorpiones)***
Withius gracilipalpus Mahnert, 1988 (Pseudoscorpiones)***
Withius nanus Mahnert, 1988 (Pseudoscorpiones)***
Zaona cavicola Mahnert, 2001 (Pseudoscorpiones)

Appendix 3: Taxa dedicated to Volker Mahnert

Animal genera

Mahnertella Mahunka, 1997 (currently in the synonymy of
Rugoppia Mahunka, 1986; Acari)
Mahnertius Harvey & Muchmore, 2013 (Pseudoscorpiones)
Mahnertozetes Mahunka & Mahunka-Papp, 2009 (Acari)

Animal species

Acanthocreagris mahnerti Dumitresco & Orghidan, 1986
(Pseudoscorpiones)
Acritus mahnerti Gomy, 1981 (Coleoptera)
Akyttara mahnerti Jocqué, 1987 (Araneae)
Allochernes mahnerti Georgescu & Căpuse, 1996
(Pseudoscorpiones)
Allolobophora handlirschi mahnerti Zicsi, 1973 (currently in
Aporrectodea; Oligochaeta)
Americhernes mahnerti Harvey, 1990 (Pseudoscorpiones)
Apimela mahnerti Pace, 1996 (Coleoptera)
Atheta mahnerti Pace, 1995 (Coleoptera)
Ausobskya mahnerti Silhavý, 1976 (Opiliones)
Bothriechis mahnerti Schätti & Kramer, 1991 [currently in
the synonymy of *Bothrops punctatus* (Garcia, 1896);
Serpentes]
Camillina mahnerti Platnick & Murphy, 1987 (Araneae)
Catharosoma mahnerti Golovatch, 2005 (Diplopoda)
Centruroides mahnerti Lourenço, 1983 (Scorpiones)
Chactas mahnerti Lourenço, 1995 (Scorpiones)
Chthonius (Ephippiochthonius) mahnerti Zaragoza, 1984
(Pseudoscorpiones)
Ctenobelba mahnerti Mahunka, 1974 (Acari)
Cypha mahnerti Pace, 1994 (Coleoptera)
Delamarea mahnerti Leleup, 1983 (Coleoptera)
Dendrobaena mahnerti Zicsi, 1974 (Oligochaeta)
Dolicheremaeus mahnerti Mahunka & Mahunka-Papp, 2009
(Acari)
Drusilla mahnerti Pace, 1996 (Coleoptera)
Edaphus mahnerti Puthz, 1990 (Coleoptera)
Elgonidium mahnerti Bonadona, 1978 (Coleoptera)
Embuana mahnerti Heiss & Baňář, 2016 (Heteroptera)
Epipleuria mahnerti Fürsch, 2001 (Coleoptera)
Glossodrilus mahnerti Zicsi, 1989 (Oligochaeta)
Guaraniella mahnerti Baert, 1984 (Araneae)
Gyrophæna mahnerti Pace, 1994 (Coleoptera)
Helladocampa mahnerti Condé, 1984 (Diplura)

Hemigrammus mahnerti Uj & Géry, 1989 (Pisces)
Holoparasitus mahnerti Juvara-Bals, 2008 (Acari)
Leleupiozethus mahnerti Coulon, 1979 (Coleoptera)
Magellozetes mahnerti Mahunka, 1984 (currently in the
synonymy of *Ceratozetes platyrhinoides* Hammer,
1961; Acari)
Megarthrus mahnerti Cuccodoro & Löbl, 1995 (Coleoptera)
Metanapis mahnerti Brignoli, 1981 (Araneae)
Microdipnites mahnerti Garetto & Giachino, 1999
(Coleoptera)
Microplana mahnerti Minelli, 1977 [currently in the
synonymy of *Microplana terrestris* (O.F. Müller,
1773); Tricladida]
Neobisium mahnerti Heurtault, 1980 (Pseudoscorpiones)
Occidenchthonius mahnerti Zaragoza, 2017
(Pseudoscorpiones)
Oedichirus mahnerti de Rougemont, 2018 (Coleoptera)
Oonops mahnerti Brignoli, 1974 (Araneae)
Paracoryza mahnerti Balkenohl, 2000 (Coleoptera)
Paratemnus mahnerti Sivaraman, 1981 (currently in
Paratemnoides; Pseudoscorpiones)
Paratricommatus mahnerti Soares & Soares, 1985 (Opiliones)
Proteocephalus mahnerti de Chambrier & Vaucher, 1999
(Cestoda)
Ptychadena mahnerti Perret, 1996 (Amphibia)
Roncus mahnerti Ćurčić & Beron, 1981 (Pseudoscorpiones)
Scaphoxium mahnerti Löbl, 2010 (Coleoptera)
Scheloribates mahnerti Mahuka & Mahunka-Papp, 2008
(Acari)
Schistura mahnerti Kottelat, 1990 (Pisces)
Scutacarus mahnerti Mahunka, 1972 (Acari)
Sprentascaris mahnerti Petter & Cassone, 1984 [currently in
Raphidascaris (Sprentascaris); Nematoda]
Stenohya mahnerti Schawaller, 1994 (Pseudoscorpiones)
Trichouropoda mahnerti Kontschán, 2015 (Acari)
Zodarion mahnerti Brignoli, 1984 [currently in the synonymy
of *Zodarion emarginatum* (Simon, 1873); Araneae]
Zyras (Pycnodonia) mahnerti Pace, 1996 (Coleoptera)

Mineral

Mahnertite [described and named in 1996 by Halil Sarp (former curator of the Department of Minerology in the MHNG) from a mine near Toulon in southern France].

A new species of reed snake, *Calamaria* Boie, 1827 from the Central Highlands of Vietnam (Squamata: Colubridae)

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Abstract: A new species of *Calamaria* Boie, 1827 is described based on a single specimen collected in evergreen forest at 1240 m elevation of Ta Dung Nature Reserve in Dak Nong Province, Central Vietnam. The new species is characterized by (1) rostral wider than high; (2) paraparietal surrounded by six shields and scales; (3) eye diameter larger than eye-mouth distance; (4) preocular present; (5) supralabials 5/4, 3-4/2-3 entering orbit; (6) maxillary teeth nine, modified; (7) infralabials 5/4, first three touching anterior chin shields; (8) mental touching tip of right anterior chin shield; (9) ventrals 1 + 174; subcaudal scales 18/17, divided; (10) precloacal plate single; (11) tail relatively short (6.2% of the total length), nearly as thick as body, slightly tapering, and ending in obtuse point; (12) dorsal scales reducing to six rows at position above 4th subcaudal, and to four rows above 13th subcaudal on tail; (13) dorsum dark with irregular yellow blotches; and (14) ventral side dark with few yellow blotches and bands. This is the sixth new *Calamaria* species described from Vietnam in the past thirteen years and the tenth species of *Calamaria* recorded from this country.

Keywords: *Calamaria* - Serpentes - taxonomy - Dak Nong Province - Vietnam.

INTRODUCTION

Calamaria Boie, 1827 is a burrowing, forest-dwelling snake genus, which represents one of the most successful Southeast Asian genera of colubrids. Reed snakes can be found from eastern China and the Ryukyu Islands in the north, through Vietnam, Laos, Cambodia, Thailand and the Malaysian Peninsula to Myanmar in the west, and southward to Sulawesi, Seram and the Philippines (Uetz *et al.*, 2018). Although being a diverse genus, *Calamaria* species exhibit a rather homogenous morphology. Inger & Marx (1965) recognized a total of 50 species of *Calamaria*, with nine taxa being described therein as new species or subspecies. Since their systematic review, ten new taxa have been discovered: *C. lovii*

ingermarxorum Darevsky & Orlov, 1992 from central Vietnam; *C. ingeri* Grismer, Kaiser & Yaakob, 2004 from West Malaysia; *C. thanhi* Ziegler & Le, 2005 from central Vietnam; *C. butonensis* Howard & Gillespie, 2007, and *C. longirostris* Howard & Gillespie, 2007 from Buton Island, Indonesia; *C. banggaiensis* Koch, Arida, McGuire, Iskandar & Böhme, 2009 from Banggai Island, Indonesia; *C. gialaiensis* Ziegler, Nguyen & Nguyen, 2008; *C. abramovi* Orlov, 2009; *C. sangi* Nguyen, Koch & Ziegler, 2009; *C. concolor* Orlov, Nguyen, Nguyen, Ananjeva & Ho, 2010, the latter four all being discovered in central Vietnam. In addition, *C. pfefferi* Stejneger, 1901 was recently listed as a synonym of *C. pavimentata* Duméril, Bibron & Duméril, 1854 (Wallach *et al.*, 2014).

During recent field surveys in the Central Highlands of Vietnam, an eye-catching, ground-dwelling snake was discovered. Morphological examination of the specimen from Ta Dung Nature Reserve in Dak Nong Province revealed it to be a representative of the genus *Calamaria*. Diagnostic characters are the dorsal scales in 13 rows throughout body, internasals and prefrontals fused, and parietal broadly in contact with supralabials (Inger & Marx, 1965). Because the specimen was neither assignable to any of the reed snakes known from Vietnam nor to species reported from neighboring countries, we herein describe it as a new species.

MATERIAL AND METHODS

Sampling: This study is based on a single specimen, which was euthanized in a closed vessel with a piece of cotton wool containing ethyl acetate (Simmons, 2002), fixed in 85% ethanol and subsequently stored in 70% ethanol. The specimen was deposited in the herpetological collection of the Institute of Ecology and Biological Resources (IEBR), Vietnamese Academy of Science and Technology, Hanoi, Vietnam.

Morphological examination: Identification of sex was performed by dissection (inspection of gonads). Snout-vent length and tail length were taken after preservation with a measuring tape. The number of ventral scales was counted according to Dowling (1951). The numbers of dorsal scale rows are given at one head length behind head, at midbody, and at one head length before vent. Maxillary teeth were counted by examining the right maxilla. Scallation and maxillary teeth numbers were studied using a binocular dissecting microscope. We herein use the term precloacal instead of anal. Bilateral values were given as left / right. Methods and comparisons followed Inger & Marx (1965), Ziegler *et al.* (2008), and Nguyen *et al.* (2009).

Abbreviations of morphological characters used in the text are as follows: – *Measures and ratios*: – SVL: snout-vent length (from tip of snout to anterior margin of cloaca). – TaL: tail length (from posterior margin of cloaca to tip of tail). – TL: total length (SVL + TaL). – TaL/TL: ratio tail length/total length.

RESULTS

Calamaria dominici Ziegler, Tran & Nguyen sp. nov.

Figs 1–4

Holotype: IEBR A.2018.1, an adult female collected on 28 May 2017 at 11:30 on a forest path by Anh Vu Tran in evergreen mixed forest of broadleaf and conifer trees within Ta Dung Nature Reserve, Dak Nong Province, Central Highlands, Vietnam, at an elevation of 1240 m asl.

Diagnosis: A species of the genus *Calamaria* characterized by the combination of the following characters:

- (1) rostral wider than high;
- (2) paraparietal surrounded by six shields and scales;
- (3) eye diameter larger than eye-mouth distance;
- (4) preocular present;
- (5) supralabials 5/4, 3-4/2-3 entering orbit;
- (6) maxillary teeth nine, modified;
- (7) infralabials 5/4, first three touching anterior chin shields;
- (8) mental touching tip of right anterior chin shield;
- (9) ventrals 1 + 174; subcaudal scales 18/17, divided;
- (10) precloacal plate single;
- (11) tail relatively short (6.2% of the total length), nearly as thick as body, slightly tapering, and ending in obtuse point;
- (12) dorsal scales reducing to six rows at position above 4th subcaudal, and to four rows above 13th subcaudal on tail;
- (13) dorsum dark with irregular yellow blotches; and
- (14) ventral side dark with few yellow blotches and bands.

Description of holotype: Habitus vermiform; head indistinct from neck; pupil round; tail relatively short (6.2% of the total length), nearly as thick as body, slightly tapering, ending in obtuse point.

Size. SVL: 395 mm; TaL: 26 mm; TL: 421 mm; ratio TaL/TL: 0.06.

Dentition. Right upper maxilla with 9 modified maxillary teeth.

Body scalation. Dorsal scale rows 13–13–13, smooth. Dorsal scales reducing to six rows at position above fourth subcaudal, to five rows above 12th subcaudal, and to four rows above 13th subcaudal on tail.

174 ventrals (+ 1 preventral); 18/17 subcaudals, all paired, first pair not in contact, followed by tail tip; precloacal single.

Head scalation. Rostral wider than high, portion visible from above shorter than prefrontal suture. Prefrontal shorter than frontal, not entering orbit, and touching first two supralabials on right side and second and third supralabial on left side. Frontal hexagonal, nearly two times maximum width of supraocular. Paraparietal surrounded by six shields and scales. Length of parietal shorter than distance from posterior tip of frontal to posterior tip of rostral. Supraocular 1/1. Loreal 1/1. Preocular 1/1, distinctly higher than wide. Postocular 1/1, higher than wide, not as high as eye diameter. Eye diameter larger than eye-mouth distance. 5/4 supralabials, on left side third and fourth entering orbit, fifth longest; on right side second and third entering orbit, fourth longest. Mental triangular, touching tip of right anterior chin shields. 5/4 infralabials, first three touching anterior chin shields. First pair of chin shields in contact mesially, second pair touching anteriorly and separated posteriorly.

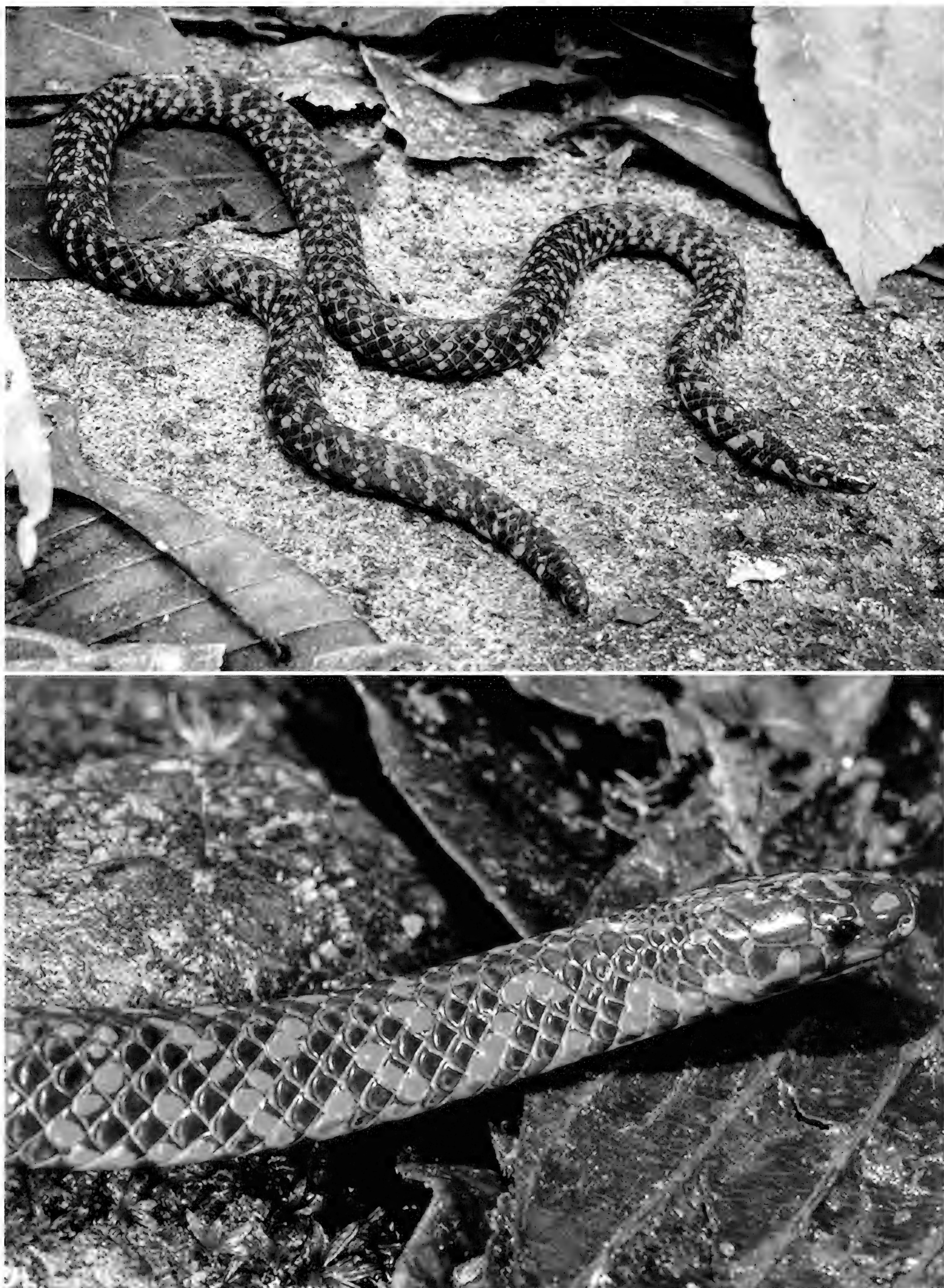


Fig. 1. Holotype of *Calamaria dominici* sp. nov. (IEBR R.2018.1) in life. Photos R. D. Babb.

Coloration (in life). Eye black; tongue grey anteriorly, pinkish-grey posteriorly; dorsum of body and tail dark purplish-black, iridescent; head with irregular small and few medium-sized yellow blotches; body with medium-sized to large yellow blotches, irregularly arranged, in part forming transverse or oblique rows, sometimes in zig-zag pattern; hind part of body dorsum and dorsal surface of tail less intensely blotched; venter purplish-black with irregular yellow transverse bands or blotches; chin and throat region dark with yellow reticulation or blotches and bands; lower tail surface dark with few yellow blotches or bands.

Coloration (in preservative). Ground colour purplish-black to brownish-black with whitish-cream pattern of irregularly arranged blotches.

Comparisons: Comparisons of the new species with its congeners took place based on the following references (Inger & Marx, 1965; Grismer *et al.*, 2004, Howard & Gillespie, 2007, Ziegler *et al.*, 2008; Koch *et al.*, 2009; Nguyen *et al.*, 2009; Orlov, 2009; Orlov *et al.*, 2010). In the following we first compare *Calamaria dominici* sp. nov. with the *Calamaria* species reported to occur in Vietnam:

Calamaria dominici sp. nov. already differs by its color pattern from the species known from Vietnam: *C. abramovi* has a black dorsum without spots, the venter is covered with yellow-orange spots; *C. buchi* is blackish above with each dorsal scale having small light spots and its ventral scales having dark outermost corners; *C. concolor* has a uniform, patternless light brown body dorsum and a cream venter; *C. gialaiensis* has a light greyish brown dorsum with an indistinct dark neck collar and few dark blotches along posterior vertebral region, two pairs of light blotches on the tail, as well as a yellowish beige ventral side, with dark outermost corners of ventrals and anterior subcaudals; *C. pavimentata* usually has narrow, dark, longitudinal stripes, and a solid black collar behind the neck; *C. sangi* has a greyish brown dorsum with fine dark mottling, as well as a yellowish beige ventral side, with dark transverse bands and a dark longitudinal stripe below the tail; *C. septentrionalis* has dorsal scales with many small light dots forming a network; *C. lovii ingermarxorum* has an immaculate grey-bluish dorsum with light spots on each side of the neck covering four scales; and *C. thanhi* has distinct transverse light body bands.

Calamaria dominici sp. nov. further differs from the



Fig. 2. Head views of the holotype of *Calamaria dominici* sp. nov. (IEBR R.2018.1) in life. Photos R. W. Van Devender.

species so far known from Vietnam in morphological characters:

Calamaria dominici sp. nov. differs from *C. abramovi* Orlov, 2009 by its rostral being wider than high (versus its height equal to width), by the dorsal scales reducing to four rows above 13th subcaudal on tail (versus above 20th subcaudal in the female holotype of *C. abramovi*), by 18/17 versus 20 subcaudals in females, and by having 13-13-13 versus 12-13-13 dorsal scale rows.

Calamaria dominici sp. nov. differs from *C. buchi* Marx & Inger, 1955 by having fewer ventral scales in females (1 + 174 versus 221-236 in *C. buchi*), by the rostral being wider than high (versus rostral higher than wide), by the dorsal scales reducing to four rows above 13th subcaudal on tail (versus above 3rd-4th subcaudal), by 18/17 versus 13-14 subcaudals in females, by having a ratio of tail length to total length of 6.2% (versus 3.9-4.1 in female *C. buchi*), and by the length of parietal being shorter than distance from posterior tip of frontal to posterior tip of rostral (versus length of parietal greater than distance from posterior tip of frontal to posterior tip of rostral).

Calamaria dominici sp. nov. differs from *C. concolor* Orlov, Nguyen, Nguyen, Ananjeva & Ho, 2010 by having paraparietal surrounded by six shields and scales

(versus by five shields and scales), and by the dorsal scales reducing to four rows above 13th subcaudal on tail (versus above 19th subcaudal in the male holotype of *C. concolor*).

Calamaria dominici sp. nov. differs from *C. gialaiensis* Ziegler, Nguyen & Nguyen, 2009 by having paraparietal surrounded by six shields and scales (versus by five shields and scales), and by tail ending in obtuse point (versus with rounded end).

Calamaria dominici sp. nov. differs from *C. lovii* Boulenger, 1887 by having a preocular scale (versus being absent in *C. lovii*), and by tail ending in obtuse point (versus with blunt end in the subspecies occurring in Vietnam, *C. lovii ingermarxorum*).

Calamaria dominici sp. nov. differs from *C. pavementata* Duméril, Bibron & Duméril, 1854 by the rostral being wider than high (versus rostral as broad as high or slightly higher than broad), and by the tail ending in obtuse point (tail tip with sharp point in *C. pavementata*).

Calamaria dominici sp. nov. differs from *C. sangi* Nguyen, Koch & Ziegler, 2009 by having fewer ventral scales (1 + 174 versus 2 + 190 in *C. sangi*), and by the dorsal scales reducing to six rows above 4th subcaudal on tail (versus above 8th subcaudal).

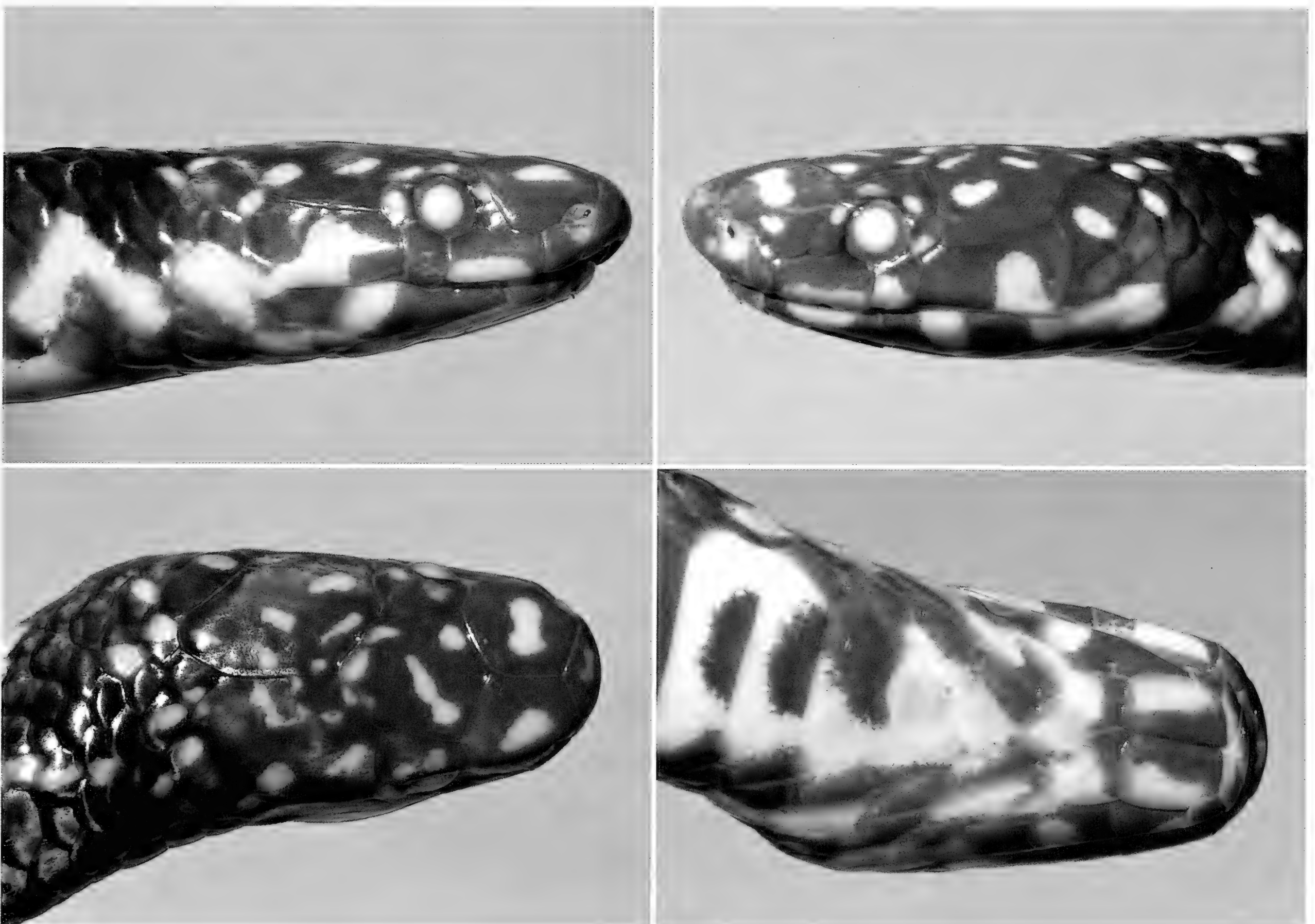


Fig. 3. Head views of the preserved holotype of *Calamaria dominici* sp. nov. (IEBR R.2018.1). Photos T. Ziegler.

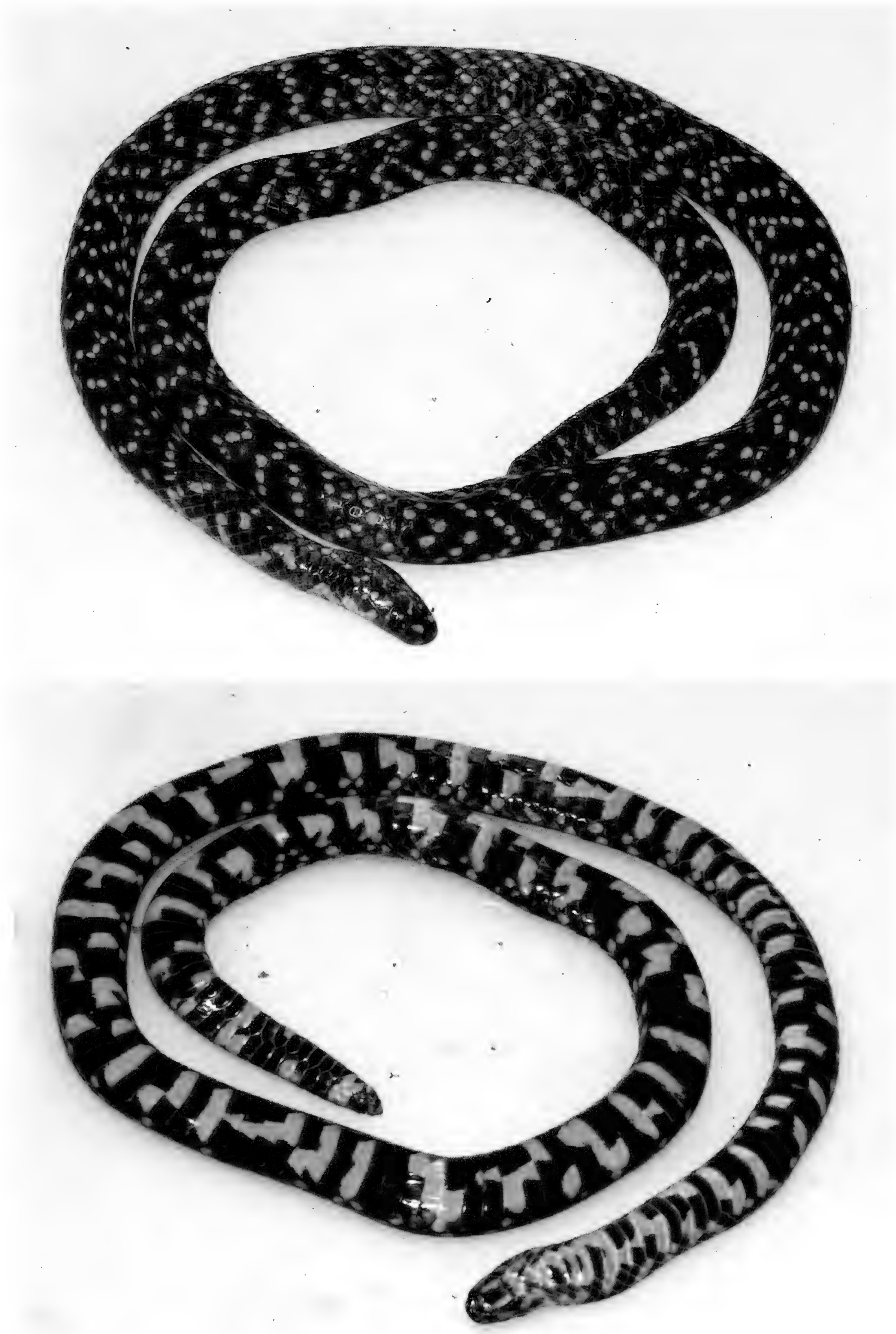


Fig. 4. Dorsal and ventral views of the holotype of *Calamaria dominici* sp. nov. (IEBR R.2018.1). Photos R. W. Van Devender.

Calamaria dominici sp. nov. differs from *C. septentrionalis* Boulenger 1890 by 18/17 versus 6-11 subcaudals in females, by having a ratio of tail length to total length of 6.2% (versus 2.6-4.3 in female *C. septentrionalis*), and by the tail ending in obtuse point (versus tail tip rounded in *C. septentrionalis*).

Calamaria dominici sp. nov. differs from *C. thanhi* Ziegler & Le, 2005 by having a preocular scale (versus absent), by having fewer ventral scales (1 + 174 versus 198 in *C. thanhi*), and by the tail ending in obtuse point (tail tip with sharp point in *C. thanhi*).

Calamaria dominici sp. nov. differs from *C. yunnanensis* Chernov, 1962, a species reported from southern China, which was judged as a doubtful form by Inger & Marx (1965), but subsequently listed as valid by Yang & Inger (1986) and Zhao & Adler (1993), by having a preocular (versus being absent), and by lacking narrow, dark, elongated stripes along the body.

Calamaria dominici sp. nov. has a distinct preocular scale, which is lacking in the following species: *C. alidae* Boulenger, 1920, *C. apraeocularis* Smith, 1927, *C. banggaiensis* Koch, Arida, McGuire, Iskandar & Böhme, 2009, *C. butonensis* Howard & Gillespie, 2007, *C. ceramensis* De Rooij, 1913, *C. gracillima* (Günther, 1872), *C. javanica* Boulenger, 1891, *C. longirostris* Howard & Gillespie, 2007, *C. mecheli* Schenkel, 1901, *C. rebentischi* Bleeker, 1860, and *C. schmidtii* Marx & Inger, 1955.

Calamaria dominici sp. nov. has modified maxillary teeth and thus differs from the following species, which have unmodified maxillary teeth: *C. acutirostris* Boulenger, 1896, *C. curta* Boulenger, 1896, *C. lautensis* De Rooij, 1917, *C. leucogaster* Bleeker, 1860, and *C. ulmeri* Sackett, 1940.

Calamaria dominici sp. nov. has paraparietal surrounded by six shields and scales and thus differs from *C. albiventer* (Gray, 1835) (5), *C. bicolor* Duméril, Bibron & Duméril, 1854 (5), *C. bitorques* Peters, 1872 (5), *C. brongersmai* Inger & Marx, 1965 (5), *C. everetti* Boulenger, 1893 (5), *C. griswoldi* Loveridge, 1938 (5), *C. hilleniusi* Inger & Marx, 1965 (5), *C. joloensis* Taylor, 1922 (5), *C. lateralis* Mocquard, 1890 (5), *C. lumbricoidea* Boie, 1827 (4 or 5), *C. lumholtzi* Andersson, 1923 (5), *C. muelleri* Boulenger, 1896 (5), *C. palavanensis* Inger & Marx, 1965 (5), *C. prakkei* Lidth de Jeude, 1893 (5), and *C. suluensis* Taylor, 1922 (5).

Calamaria dominici sp. nov. differs from the following species by a distinctly higher ventral scale count in the female sex: *C. abstrusa* Inger & Marx, 1965 (145-152), *C. crassa* Lidth de Jeude, 1922 (158-164), *C. eiselti* Inger & Marx, 1965 (151-153), *C. linnaei* Boie, 1827 (148-166), and *C. melanota* Jan, 1862 (131-154).

Calamaria dominici sp. nov. differs from the following species by a distinctly higher subcaudal scale count in the female sex: *C. margaritophora* Bleeker, 1860 (8-11), *C. nuchalis* Boulenger, 1896 (9), and *C. sumatrana* Edeling, 1870 (10-14).

Calamaria dominici sp. nov. differs from *C. grabowskyi*

Fischer, 1885 by a distinctly lower subcaudal scale count in the female sex (20-28).

Calamaria dominici sp. nov. has the first three infralabials touching the anterior chin shields versus only two pairs of infralabials touching anterior chin shields in *C. borneensis* Bleeker, 1860.

In addition, *Calamaria dominici* sp. nov. differs from the remaining species at least by a distinct colour pattern: *C. battersbyi* Inger & Marx, 1965 (with narrow longitudinal stripes mid-dorsally), *C. oesemani* Inger & Marx, 1965 (with a continuous light stripe the entire length of the body), *C. doederleini* Gough, 1902 (with narrow dark brown crossbands on body and tail), *C. forcarti* Inger & Marx, 1965 (with narrow dark crossbands behind head, body without stripes, venter yellow), *C. gervaisii* Duméril, Bibron & Duméril, 1854 (usually with a dark-edged, interrupted, light stripe on first body scale row), *C. ingeri* Grismer, Kaiser & Yaakob, 2004 (with incomplete light transverse bands on body and tail), *C. modesta* Duméril, Bibron & Duméril, 1854 (with ventrals having dark pigment at least laterally), *C. schlegeli* Duméril, Bibron & Duméril, 1854 (dark above, light below, head yellow above and below or black above and yellow below, or intermediate conditions), *C. virgulata* Boie, 1827 (dorsally dark brown, each scale with a light network, with or without longitudinal dark stripes).

Etymology: Named *dominici* to honor Dominic T. Charles Scriven, founder of Wildlife at Risk (WAR), for his contribution towards wildlife conservation in Vietnam.

Suggested common names: Dominic's reed snake (English), Ran mai gam do-mi-nic (Vietnamese), Calamaire de Dominic (French), and Dominics Zwergschlange (German).

Distribution: *Calamaria dominici* is currently known only from the type locality (Fig. 5).

Natural history: The holotype was found in evergreen mixed forest of broadleaf and conifer trees. The snake was discovered on a forest path near a small creek, for about 50 m distance from a large creek (Figs 6-7). It was found, surface active, in a densely vegetated boggy area at 11:30. The surrounding habitat was primary forest consisting of dense understory punctuated with large boulders scattered over a ca. 20° slope that descended to a large creek. Dissection of the female holotype revealed ovaries with some eggs enlarge to 4 mm.

DISCUSSION

Calamaria are fossorial snakes and difficult to find. Thus, often only single individuals are available so that descriptions must be based on a single type specimen, as in the present case. Other such examples are *C. thanhi* and *C. abramovi* (Ziegler & Le, 2005; Orlov, 2009).

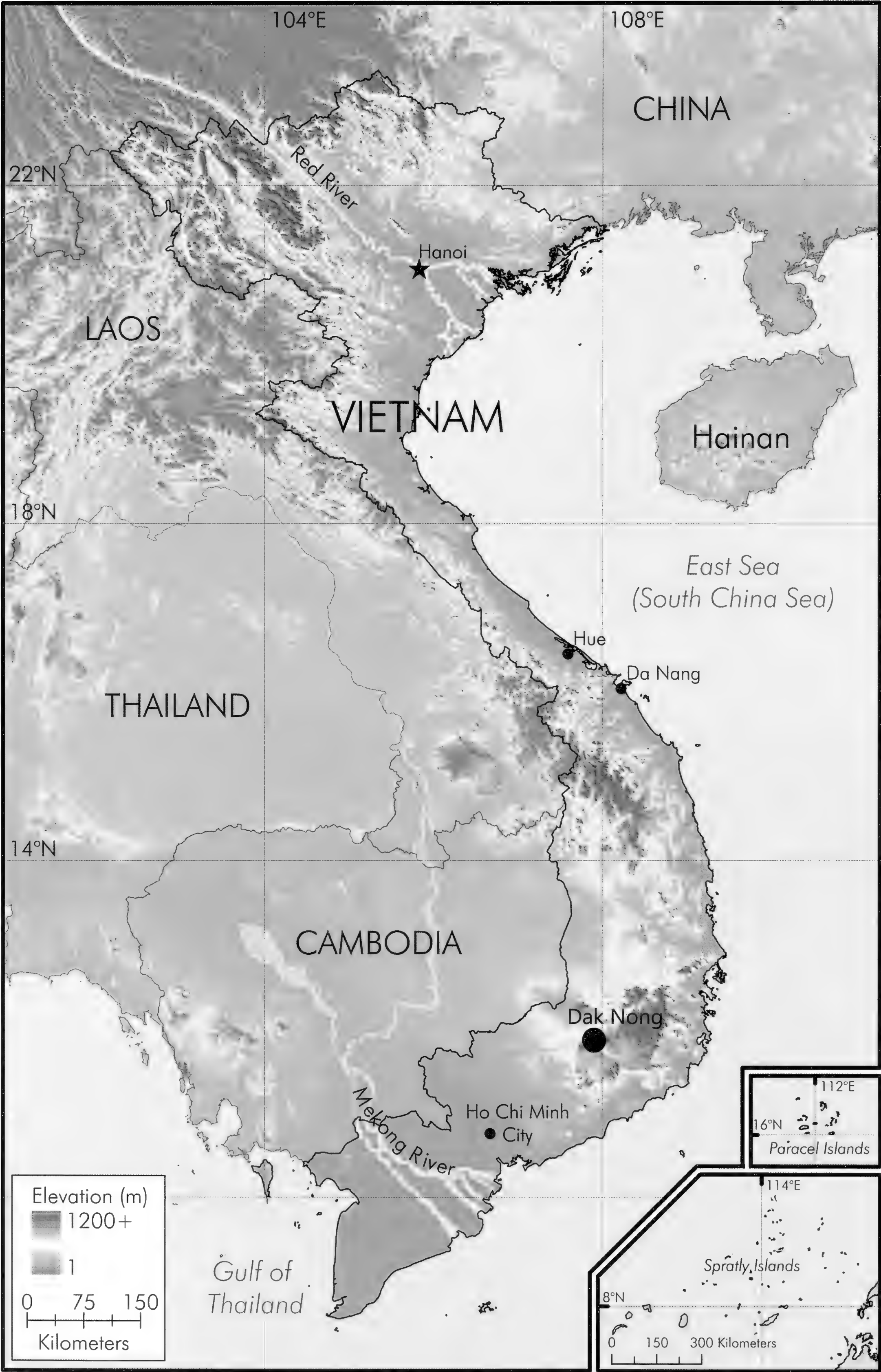


Fig. 5. Map of Vietnam with the type locality (large black dot) of *Calamaria dominici* sp. nov. in Ta Dung Nature Reserve, Dak Nong Province.



Fig. 6. Ta Dung Nature Reserve, Dak Nong Province, Central Highlands, Vietnam. Photo V. A. Tran.



Fig. 7. Habitat of *Calamaria dominici* sp. nov. in Ta Dung Nature Reserve, Dak Nong Province, Central Highlands, Vietnam. Photo R. D. Babb.

Inger & Marx (1965) defined the Great Sunda Archipelago, namely the Borneo-Sumatra region, as principle center of evolution and dispersal of the genus *Calamaria*, since it was home for more than 60% of the species known at that time. With six new *Calamaria* species having been described from Vietnam in the past 13 years, this country also seems to play a major role in reed snake diversification. With ten species of *Calamaria* recorded from Vietnam, this country now houses more than 16% of the 60 currently recognized species.

The megophryid anuran *Leptolalax tadungensis* Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016, now *Leptobranchella tadungensis* (see Chen *et al.*, 2018), is another recently described species from Ta Dung Nature Reserve, the type locality of *Calamaria dominici*. Also this recent frog discovery represents an endemic species for Ta Dung Nature Reserve (Rowley *et al.*, 2016). The conservation importance of this unique Nature Reserve is also underscored by the recent discovery of endemic plants such as *Aristolochia tadungensis* Do, Luu, Wanke & Neinhuis, 2015, a Pelican Flower from Ta Dung Nature Reserve (Do *et al.*, 2015).

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Phylogenetic notes on the rare Mediterranean digger wasp *Psenulus fulvicornis* (Schenck, 1857) (Hymenoptera: Crabronidae) new to Switzerland

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Abstract: Identifying alien species is important to detect invaders early and to survey shifts in species ranges in the context of global change. Here we present the first recorded occurrences of the Mediterranean digger wasp *Psenulus fulvicornis* (Schenck, 1857) (Crabronidae) in Switzerland. To aid species identification and separation from the morphologically similar congener *P. schencki* (Tournier, 1889), which is known to occur in Switzerland, we show discriminating morphological characters and deliver the first DNA barcode sequences and a molecular phylogenetic tree of the mitochondrial *cox1* locus from specimens sampled at the European scale. While the species can be readily separated by morphological characters, maximum likelihood and Bayesian inferred phylogenetic trees revealed the existence of polyphyly. Thus, we could not identify a barcoding gap at the European scale, which may hamper taxon identification. Nevertheless, *cox1* sequences were diagnostic for all Central European specimens. Finally, an exhaustive revision of *P. schencki* accessions in the Swiss historical museum and private collections did not reveal overlooked specimens of *P. fulvicornis*. This confirms the status of *P. fulvicornis* as a new species to Switzerland, where it is currently only known from the Cantons of Zurich and Geneva; inhabiting warm lowland habitats such as urban gardens.

Keywords: Alien species - Cytochrome oxidase 1 - first record - Hymenoptera - identification - introduction - invasive - urban garden.

INTRODUCTION

Tous les entomologistes qui ont tenté de déterminer des hyménoptères appartenant au groupe des Psenini ont pu se rendre compte des difficultés que présente ce travail.

Jacques de Beaumont (1937-1939)

Diversity and distribution of organisms across taxonomic groups are changing at fast rates worldwide (e.g. Pereira *et al.*, 2010). The correct identification of new arrivals is important: not only to conduct risk assessments of

potential pest organisms at an early stage of invasion, but also to elucidate range shifts of non-invasive species in the context of global change (e.g. climate change or urbanization; Blackburn *et al.*, 2011; Simberloff *et al.*, 2013; Hawkins *et al.*, 2015).

Cities are port of entries for alien species due to extensive trade, traffic and transport, which can facilitate (long distance) dispersal (Rebele, 1994; von der Lippe & Kowarik, 2007). Moreover, climatic barriers limiting the establishment and spread of such species may be overcome due to the urban heat island effect (Kowarik,

2011; Aronson *et al.*, 2016). For instance, surveys of urban arthropod communities in northern temperate cities frequently reveal new alien species that originate from warmer climates (e.g. Germann *et al.*, 2015; Frey *et al.*, 2016; Zanetta *et al.*, 2016). One prerequisite for assessing naturalization status and/or environmental impact of such species is their rapid detection and identification (Comtet *et al.*, 2015).

DNA barcoding of the mitochondrial *cox1* locus can be a simple and cost-effective method to detect and identify alien organisms: especially arthropods. For example, it may enable their identification during life stages in which determination based on morphology is difficult (Comtet *et al.*, 2015). However, this approach needs a reference database composed of barcode sequences of correctly determined voucher specimens against which unknown specimens can be compared (e.g. the Barcode of Life Data System BOLD, Ratnasingham & Hebert, 2007). Moreover, several methodological (e.g. sampling scale and intensity) and evolutionary factors (e.g. introgression) can limit the diagnostic ability of the *cox1* marker (Funk & Omland, 2003; Meyer & Paulay, 2005; DeSalle *et al.*, 2005; Petit & Excoffier, 2009; Nicholls *et al.*, 2012; Patten *et al.*, 2015; Barley *et al.*, 2016).

Here we report the Mediterranean digger wasp *Psenulus fulvicornis* (Schenck, 1857) (Crabronidae) as a new species to Switzerland by combining genetic, morphological and historical biogeographic evidence. The species was recently found for the first time during an extensive arthropod survey in urban gardens in the city of Zurich as well as in the Canton of Geneva (Boillat, 2012), but, so far, lacked a description and entry in national faunistic databases. We provide microphotographs of the discriminating morphological characters between *P. fulvicornis* and its morphologically similar congener *P. schencki* (Tournier, 1889), which already occurs in Switzerland, and investigate, for the first time, sequences of the mitochondrial *cox1* locus of both species to infer taxon identity and phylogenetic relationships among them and other Central European *Psenulus*. Finally, to confirm its status as a new species to Switzerland, we checked Swiss *P. schencki* accessions in all major Swiss museums and private collections for potentially overlooked specimens of *P. fulvicornis*.

MATERIAL AND METHODS

Study species

The cosmopolitan genus *Psenulus* Kohl, 1897 comprises more than 160 species, with the Oriental biogeographic region being particularly species rich (Bohart & Menke, 1976; Pulawski, 2018). About 26 species occur in the Palearctic region; with eight taxa found in Central Europe and Switzerland (Bohart & Menke, 1976; Blösch, 2000; Herrmann, 2005; Artmann-Graf, 2006; Pulawski, 2018; Info Fauna, 2018).

Ecological information is available for a small number of taxa, of which all nest in hollow or pithy stems (e.g. *Sambucus* spp.) or beetle borings, and prey on adult or nymph arthropod herbivores such as aphids, leafhoppers, delphacids and psyllids (Bohart & Menke, 1976; Blösch, 2000). Some species, e.g. *P. fuscipennis* (Dahlbom, 1843), accept artificial cavities and can serve as indicators to assess the effect of land-use (change) on hymenopteran-based food-webs (e.g. Tschamntke *et al.*, 1998; Fabian *et al.*, 2013); a research approach for which DNA barcoding can be useful (Turčinavičienė *et al.*, 2016).

Psenulus fulvicornis has been reported from Algeria, Andorra, Bulgaria, Croatia, France, Germany, Greece, Hungary, Italy (Aosta), Russia, Spain, Switzerland, Syria and Turkey (Gayubo *et al.*, 2002; Schmid-Egger, 2002; Nieves-Aldrey *et al.*, 2003; Boillat, 2012; Cruz-Sanchez *et al.*, 2005; Gayubo *et al.*, 2006; Zsolt, 2008; González *et al.*, 2009; Standfuss & Standfuss, 2012; Reder & Niehuis, 2014; Yildirim *et al.*, 2015; Mokrousov & Popov, 2016) (Fig. 1). Older observations are given from Austria (Tirol), Italy (Trentino – Alto Adige) and Poland (Pomeriana) (Brischke, 1864; von Aichinger, 1870; Kohl, 1880, 1888). Taken together, these occurrences indicate a geographic range spanning from the Mediterranean to the Anatolian region, with additional occurrences in central and southern alpine valleys, and continental and steppe zones of Europe. Schmid-Egger (2002) observed a slight morphological divergence in several taxonomically important characters (e.g. the texture of the propodeal surface) between females from Algeria, Turkey and Syria on the one hand, and females from Central Europe on the other hand; a pattern which may indicate phylogeographic structuring.

In Central Europe *P. fulvicornis* is found in warm lowland habitats such as abandoned vineyards in the Upper Rhine Plain in Germany, which is a region characterized by a relatively mild climate (Blösch, 2000). In the Mediterranean area, specimens have been captured in olive and oak (*Quercus ilex* L.) groves, and vineyards. In Spain and in the North Caucasus they also occur on (shrubby) coastal sand dunes (see Results).

In the past, the taxonomic status of *P. fulvicornis* as a separate species has been doubted due to its morphological similarity with other taxa, the low number of observations and the lack of males, which have been discovered only recently (Schenck, 1861; De Beaumont, 1937-1939; Schmidt, 1971; Schmid-Egger, 2002). *Psenulus fulvicornis* type material has been studied by the latter two authors, who highlighted the close morphological relationship with *P. schencki* (Tournier, 1889) and delivered a detailed species diagnosis. Due to the close morphological relationship between the two taxa, and since *P. fulvicornis* was described first, we here refer to them as the *Psenulus fulvicornis*-Group. Currently, the status of *P. fulvicornis* as a separate species is accepted, and the taxon is included in the standard

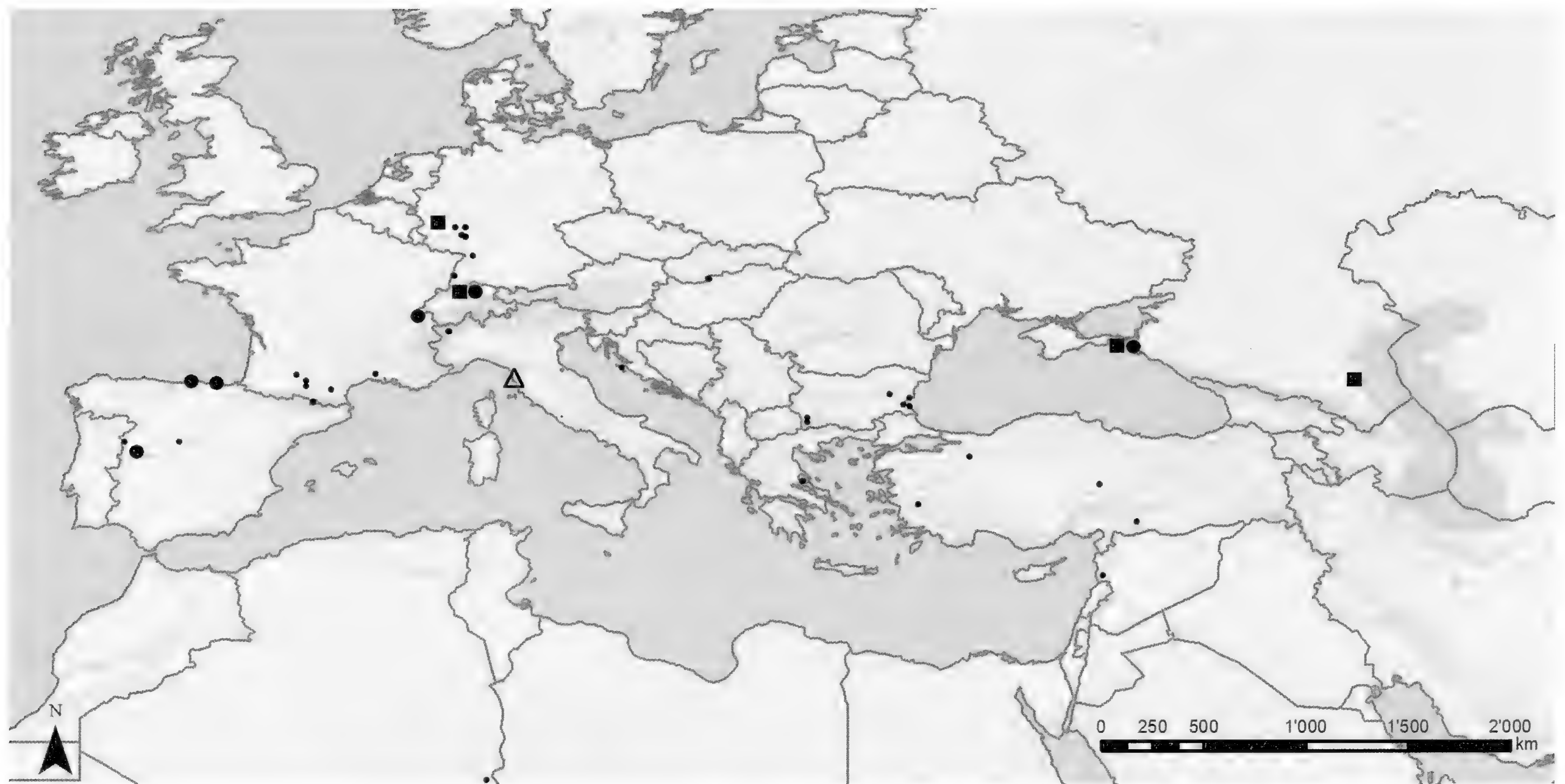


Fig. 1. Sampling sites of *Psenulus fulvicornis* (Schenck, 1857) (large filled circles) and *Psenulus schencki* (Tournier, 1889) (squares) used for the DNA barcode sequencing of the mitochondrial *cox1* locus. Small filled circles show georeferenced distribution records of *P. fulvicornis* with confirmed determinations by Schmid-Egger (2002) together with newer records by Gayubo *et al.* (2012), Mokrousov & Popov (2016), Reder & Niehuis (2014), Standfuss & Standfuss (2012) and Zsolt (2008). The triangle represents the undetermined specimen (PSC-7) from Pisa, Italy.

literature (Bohart & Menke, 1976; Blösch, 2000; Jacobs, 2007; de Jong *et al.*, 2014; Pulawski, 2018).

Psenulus fulvicornis is considered rare in Germany and red-listed under the category “Vulnerable” due to a predicted (moderate) long-term population decline (Schmid-Egger, 2010a). In contrast, the number of records has slightly increased in recent years (Schmid-Egger, 2010a, b, 2015; Frommer, 2012; Reder & Niehuis, 2014) but it is unclear whether this is due to temporary and local population size increases, for example because of exceptionally favourable weather conditions, an increased sampling effort, or whether this represents an ongoing population size increase and/or range expansion, e.g. favoured by climate warming (Schmid-Egger, 2010a).

Sampling

Flying arthropods were sampled in 85 urban gardens in the city of Zurich between May 18 and August 19 2015 with three bowl traps fixed on a triangular wooden pole. Each bowl was sprayed with either UV-bright blue, white or yellow paint (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany) (Westphal *et al.*, 2008) and three quarters filled with 0.2% Rocima solution (Acima, Buchs, Switzerland). Aculeate hymenopterans (Formicidae excluded) were identified by one of the authors (M. Řiha), and vouchers of all taxa were deposited in the reference collection

of the Swiss Federal Research Institute for Forest Snow and Landscape (WSL). One female of each of *P. fulvicornis* and *P. schencki* was caught and identified during this survey. In addition, to complete the dataset of specimens found in Switzerland, we were kindly allowed to sample one hind leg of the *P. fulvicornis* female captured in 2005 in the Canton of Geneva at the Swiss-French border (Boillat, 2012). Finally, to increase the geographic scale of the genetic analysis, specimens of both *P. fulvicornis* and *P. schencki* from areas of sympatry across almost the entire known distribution range of the *P. fulvicornis* were added from the collections of two of the authors (S. F. Gayubo and M. Mokrousov). Note that one such sample (PSC-7) from Pisa, Italy, which was originally determined as *P. schencki*, was genetically so divergent from all other samples of the *P. fulvicornis*-Group (2.3% sequence divergence over 614 base pairs) that we considered it an unknown species (see Results). Genetic analyses were further completed with publicly available *cox1* sequences of *Psenulus* taxa in GenBank and BOLD (Ratnasingham & Hebert, 2007) (supplementary Table S1 in the Appendix).

Photographs of specimens and their discriminating characters were made with a Leica Digital Microscope DVM6 by using image-stacking. Georeferenced sampling sites and distribution records were mapped with ArcGIS (version 10.2; ESRI).

DNA extraction and *cox1* sequencing

The DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) was used for the extraction following the manufacturer's instructions. The partial *cox1* locus (approx. 650 nu) was sampled using the primer pair LepF1 and LepR1 (Hebert *et al.*, 2003) following the published thermal regime. The JumpStart REDTaq ReadyMix Reaction Mix (Sigma, St. Louis, Missouri, U.S.A.) was used in the PCR, and its products were purified enzymatically using Illustra ExoProStar (GE, Chicago, Illinois, U.S.A.) following the manufacturer's instructions. PCR products were sequenced in both forward and reverse directions on an ABI 3130 sequencer (Applied Biosystems, Foster City, California, U.S.A.) using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and PCR primers, following the manufacturer's indications. The cycle sequencing products were purified using the BigDye XTerminator Purification Kit (Applied Biosystems). The corresponding forward and reverse electropherograms were assembled with CLC Main Workbench 7 (Qiagen) and visually corrected.

Genetic diversity

The *cox1* polymorphism of the *P. fulvicornis*-Group was analysed using the software DnaSP v.5.10.01 (Librado & Rozas, 2009) under the option for haploid mitochondrial DNA. No position contained gaps or missing data. Three codon positions were included with a total of 187 codon positions in the final dataset. We calculated the haplotype diversity (Hd; the probability that two randomly chosen haplotypes are different within the sample), the nucleotide diversity per site (Pi; the probability that two randomly taken nucleotides from the same position are different, and the average nucleotide differences (K). As we found that the inferred haplotypes belonged to divergent clades (see Results), genetic diversity was analysed in the entire sample (i.e. clades I-VI) and within each of the statistically well supported clades I-II (*P. fulvicornis*) and III (*P. schencki*).

Phylogenetic tree

The model of nucleotide substitutions was computed with the software jModelTest 0.1.1 (Guindon & Gascuel, 2003; Posada, 2006, 2008) and the best-fit model was selected based on the Akaike information criterion (Akaike, 1973). A maximum likelihood (ML) analysis used the RAxML-HPG BlackBox (Stamatakis, 2006) and a Bayesian analysis was performed with MrBayes 3.2.6 on the CIPRES Science Gateway (Miller *et al.*, 2010). The statistical support of branches in the ML analysis was calculated based on 1,000 bootstrap replicates (Felsenstein, 1985). Bayesian analysis was run with 5 million generations and sampled every

100th generation, following a discarded burn-in of 12,500 generations. Convergence and the consequent proportion of burn-in were assessed using Tracer v1.5 (available from <http://beast.bio.ed.ac.uk/>). Output tree files, with each containing the best tree found and labelled with the statistical support for each branch, were graphically represented with TreeGraph 2 (Stöver & Müller, 2010).

Review of Swiss museum and private collections of *P. schencki* accessions

The (undetected) presence of *P. fulvicornis* in Switzerland was checked in all major Swiss museums as well as in the most important private collections. To achieve this, we controlled the correct identification of *P. schencki* specimens since older identification keys do not discriminate the taxa (e.g. de Beaumont, 1937-1939). We followed Schmidt (1971) and Schmid-Egger (2002) for taxon identification. The subsequent collections were visited or contacted: Bündner Naturmuseum, ETH Zürich Entomological Collection (ETHZ), Muséum d'histoire naturelle de Genève (MHNG), Muséum d'histoire naturelle de Neuchâtel, Musée de la nature de Sion, Musée de zoologie, Lausanne (MZL), Museo cantonale di storia naturale (LUG), Naturhistorisches Museum Basel (NMB), Naturhistorisches Museum Bern (NMBE), Naturmuseum Luzern and Naturmuseum St. Gallen. Only collections harbouring *P. schencki* were visited except for the Musée de la nature de Sion, where the Crabronidae of Maurice Paul (1835-1898) were reviewed. Additionally, the following private collectors were contacted: Neumeyer, Rainer; Artmann-Graf, Georg; Müller, Andreas; Herrmann, Mike; Salzmann, Irene. The material examined is given in the Appendix.

RESULTS

Successfully barcoded material:

Psenulus fulvicornis (Schenck, 1857)

1 female; city of Zurich (CH: ZH); garden lot in the "Juchhof" allotment garden area; 47.3997°N, 8.4794°E; 395 m a.s.l.; 16.06.2015; D. Frey & A. Zanetta leg.; M. Řiha det.; R. Neumeyer conf.; WSL coll.; DNA-ID PHP16-0418; GenBank accession Nr. KY039438 (Figs 2, 3). – 1 female; Liencres dunes national parc (ESP: Cantabria); 01. – 30.06.2004; S. F. Gayubo leg. & det.; DNA-ID PFU-7; GenBank accession Nr. MG872065. – 1 female; Gametxo (ESP: Vizcaya); oak grove; 43.4054°N, 2.6722°W; ca. 160 m a.s.l.; 1 - 15.06.2004; S. F. Gayubo leg. & det.; DNA-ID PFU-8; GenBank accession Nr. MG872066. – 1 male; Miranda del Castañar, Las Madroñeras (ESP: Salamanca); vineyard; 05.2005; S. F. Gayubo leg. & det.; DNA-ID PFU-1; GenBank accession Nr. MG872062. – 1 female; Miranda del Castañar, Las

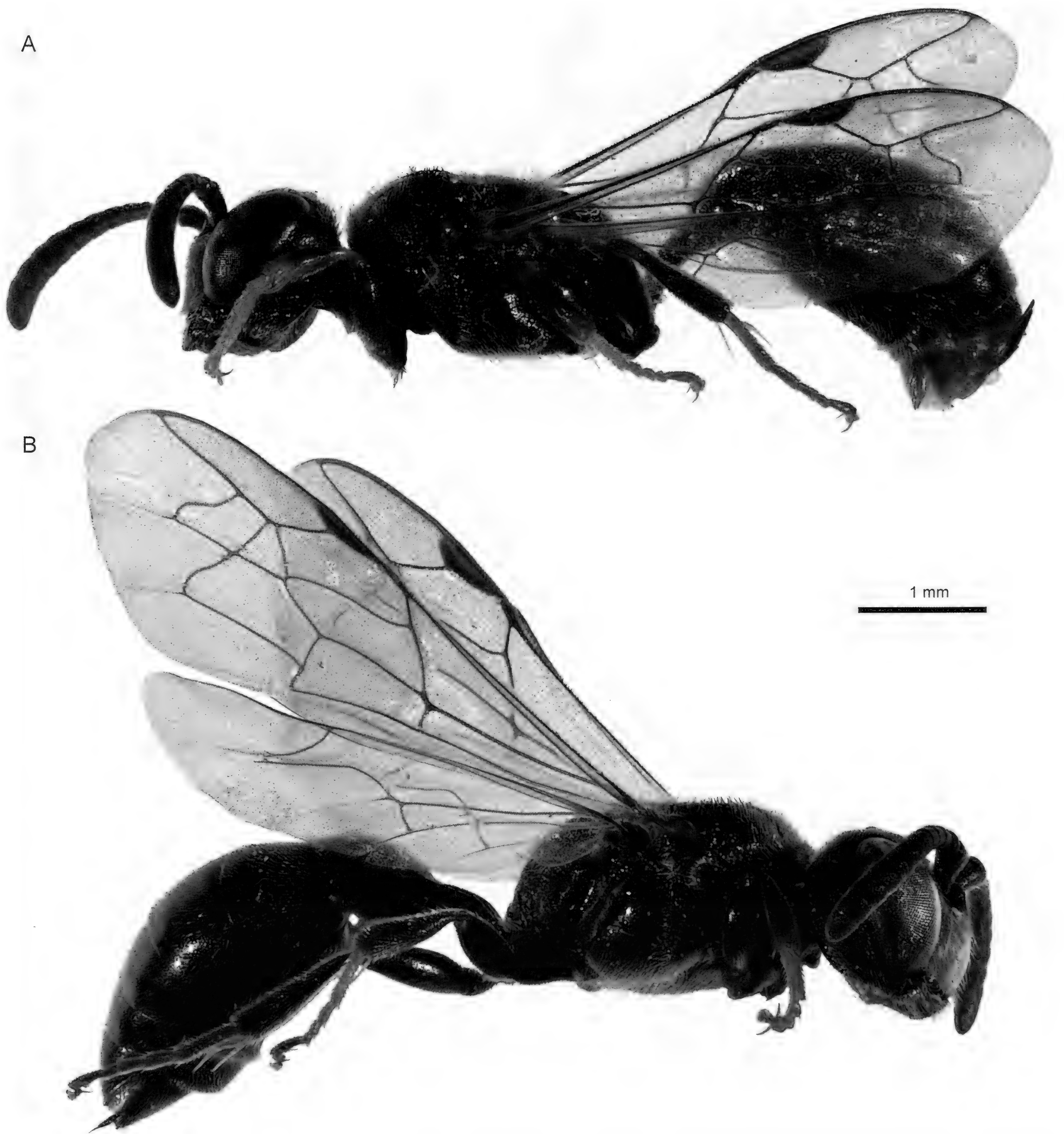


Fig. 2. (A) Female *Psenulus fulvicornis* (Schenck, 1857) from the City of Zurich, Switzerland (D. Frey & A. Zanetta leg.; M. Řiha det.; R. Neumeyer conf.; WSL coll; GenBank accession Nr. KY039438). (B) Female *Psenulus schencki* (Tournier, 1889) from the City of Zurich (25.05.2015; D. Frey & A. Zanetta leg.; M. Řiha det.; R. Neumeyer conf.; WSL coll; GenBank accession Nr. KY039439). Note the (barely visible) oblong spot at the lower end of the mid-tibia, which is a unique and shared character for both taxa among Central European *Psenulus* species (Jacobs, 2007).

Madroñeras (ESP: Salamanca); vineyard; 06.2005; S. F. Gayubo leg. & det.; DNA-ID PFU-2; GenBank accession Nr. MG872063. – 1 female; Miranda del Castañar, Las Matos (ESP: Salamanca); olive grove; 8.2005; S. F. Gayubo leg. & det.; DNA-ID PFU-3;

GenBank accession Nr. MG872064. – 1 female; Anapa, Djemete (RU: Krasnodar); shrubby coastal sand dunes; 44.961107°N, 37.281649°E; 17.06.2014; M. Mokrousov leg. & det.; DNA-ID PFU-9; GenBank accession Nr. MG872072.

Psenulus schencki (Tournier, 1889)

1 female; city of Zurich (CH: ZH); private garden; 47.3692°N, 8.5061°E, ca. 428 m a.s.l.; 25.05.2015; D. Frey & A. Zanetta leg.; M. Řiha det.; R. Neumeyer conf.; WSL coll.; DNA-ID PHP16-0493; GenBank accession Nr. KY039439 (Figs 2, 3). – 1 female; Anapa, Djemete (RU: Krasnodar); shrubby coastal sand dunes; 44.961107°N, 37.281649°E; ca. 15.06.2014; M. Mokrousov leg. & det.; DNA-ID PSC-10; GenBank accession Nr. MG872073. 1 female; Barkhan Sarykum (RU: Dagestan); on the leaves of *Ailanthus altissima*; 43.002435°N, 47.237245°E; ca. 30.05.2017; M. Mokrousov leg. & det.; DNA-ID PSC-11; GenBank accession Nr. MG872074.

Psenulus sp.

1 female; La Sterpaia, Parco San Rossore (IT: Pisa); 31.05.2005- 09.06.2005; L. Strumina leg.; S. F. Gayubo det.; DNA-ID; PSC-7; GenBank accession Nr. MG872069.

Discriminating morphological characters

The main discriminating characters between female *P. fulvicornis* and *P. schencki* are depicted in Fig. 3. In brief, the lateral surface of the propodeum of *P. fulvicornis* has short crosswise carinas that give the texture the characteristic coarse appearance (Fig. 3A). This trait is unique among females of Central European *Psenulus*. In *P. schencki* crosswise carinas are lacking, and the texture of the propodeum is smoother (Fig. 3C). Moreover, the pygidal area is usually longer and broader in *P. fulvicornis* (Fig. 3B) than in *P. schencki* (Fig. 3D). Likewise, the colour of the foretibia tends to be lighter in *P. fulvicornis* than in *P. schencki* (Fig. 2). More characters and a description of males are given by Schmid-Egger (2002) and Jacobs (2007).

cox1 sequence variation

The *cox1* sequences of *P. fulvicornis* and *P. schencki* from Zurich were sampled successfully and sequences were deposited in GenBank (supplementary Table S1 in the Appendix). However, since the *P. fulvicornis* specimen from Geneva was collected several years ago, the extracted DNA was of poor quality and *cox1* amplification failed in that sample, despite several amplification attempts with varying PCR parameters. All obtained sequences met barcode quality criteria with more than 500 bp sampled and no uncertain base calls (N's). We found 22 polymorphic sites within a 561 bp alignment of the *P. fulvicornis*-Group, which excluded gap positions on the flanking regions (Table 1). All variable sites were synonymous single-nucleotide polymorphisms (SNPs), except two nonsynonymous replacements found in the specimens from Krasnodar (Russia) and Salamanca (Spain) (Fig. 4). The overall haplotype diversity was relatively high (Table 1). The three samples from the Caucasus (clades IV, V, and VI) strongly contributed to the overall genetic diversity as each sample represented a unique haplotype and contained a large proportion of polymorphic sites (Table 1; Fig. 4).

cox1 phylogenetic tree

In total, eleven *cox1* sequences were sampled (supplementary Table S1 in the Appendix). The dataset for the analysis of the genus *Psenulus* comprised 637 nucleotide sites and 42 sequences, including five sequences of two outgroup species, *Diodontus minutus* (Fabricius, 1793) and *Pemphredon lethifer* (Shuckard, 1837). Of the 637 sites, 204 were polymorphic. Both ML and Bayesian analyses resulted in highly similar topologies for *Psenulus* species (ML tree: Fig. 5; Bayesian tree: supplementary Fig. S1 in the Appendix), and the genus obtained maximal support under both analyses. Bootstrap values and posterior probabilities were high for most taxa, but while

Table 1. *Cox1* polymorphism in the *Psenulus fulvicornis*-Group and within each of the statistically well supported Central and South-Western European clades I-II (*P. fulvicornis*) and III (*P. schencki*) based on a 561 bp alignment.

	<i>P. fulvicornis</i> -Group Clades I-VI	<i>P. fulvicornis</i> Clades I-II	<i>P. schencki</i> Clade III
Number of sequences	17	6	8
Polymorphic sites	22	7	2
Parsimony informative sites	12	4	2
Number of haplotypes (H)	11	5	3
Haplotype diversity (Hd)	0.934	0.933	0.714
Variance of haplotype diversity	0.00181	0.01481	0.01507
Nucleotide diversity per site (Pi)	0.01020	0.00606	0.00178
Average of nucleotide differences (K)	5.721	3.400	1.000

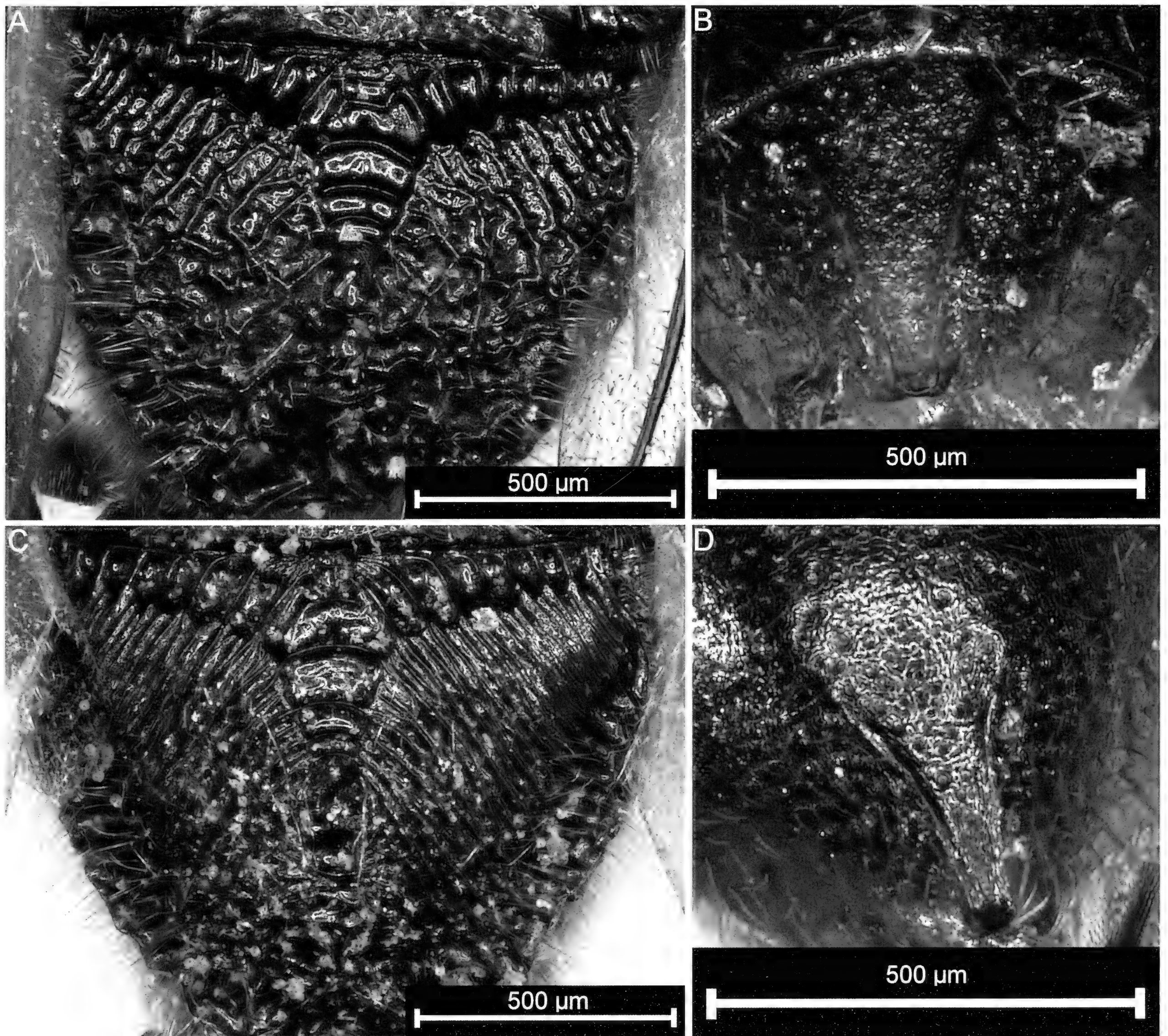


Fig. 3. Main discriminant characters between females of *Psenulus fulvicornis* (Schenck, 1857) and *P. schencki* (Tournier, 1889). (A) Propodeal surface and (B) pygidial area of *P. fulvicornis* from the City of Zurich, Switzerland (D. Frey & A. Zanetta leg.; M. Řiha det.; R. Neumeyer conf.; WSL coll; GenBank accession Nr. KY039438). (C) Propodeal surface and (D) pygidial area of *P. schencki* from the City of Zurich (25.05.2015; D. Frey & A. Zanetta leg.; M. Řiha det.; R. Neumeyer conf.; WSL coll; GenBank accession Nr. KY039439). In *P. fulvicornis*, the lateral surface of the propodeum (A) has short crosswise carinas which gives the texture coarse appearance. This character is unique among females of Central European *Psenulus*. In *P. schencki* such crosswise carinas are lacking (C), and the texture is finer. The pygidial area is longer and broader in *P. fulvicornis* (B) than in *P. schencki* (D), but this character can be difficult to observe in certain specimens.

Bayesian analysis highly supported a closer relationship between *P. pallipes*, *P. trisulcus*, *P. meridionalis* and *P. fuscipennis*, RAxML calculated only a low bootstrap value of 63% for this branching. Additionally, the position of the accession JN934379 within the *P. pallipes* clade was poorly supported in both analyses. The unidentified specimen PSC-7 from Pisa formed a highly supported sister branch to all other *P. fulvicornis* and *P. schencki* samples in both analyses (RAxML: 94%; MrBayes: 0.99), confirming the unknown status

of PSC-7 whose species identification failed with 2.3% dissimilarity from other *Psenulus* species in a BOLD System search (<http://www.boldsystems.org>; July 10th, 2018). All samples of the *P. fulvicornis*-Group formed a highly supported monophyletic clade (RAxML: 81%; MrBayes: 0.99). The samples of the *P. fulvicornis*-Group were subdivided in six clades, all of which were congruent with taxonomic boundaries based on morphology (Fig. 5): On the one hand, *P. fulvicornis* was split in two well supported clades in Central and South-

Position of segregation sites	12	45	108	111	117	144	168	178*	192	213	243	270	285	321	330	456	472*	474	486	496	516	543
PFU-1	A	G	G	T	T	G	A	A	T	A	A	G	T	A	A	T	A	C	T	A	G	
PFU-3	-	-	-	-	-	-	-	-	-	C	-	-	-	-	-	-	-	-	-	-	-	I
PFU-2	-	-	-	-	-	-	A	-	-	C	-	-	-	-	-	-	-	-	-	-	-	
PFU-7	-	-	-	-	A	-	-	-	-	C	-	G	-	-	-	-	A	-	T	-	-	II
PFU-8	-	-	-	-	A	-	-	-	-	C	-	G	-	-	-	-	A	-	T	-	-	
PHP16-0418	-	-	-	-	A	-	-	-	-	C	-	G	-	C	-	-	A	-	T	-	-	
PSC-11	-	-	-	C	A	-	-	-	-	-	-	-	-	-	-	-	A	-	T	-	G	VI
OPPFM1833	-	-	-	-	A	-	G	-	G	-	-	-	-	-	-	-	A	-	C	-	-	
OPPFM3380	-	-	-	-	A	-	G	-	G	-	-	-	-	-	-	-	A	-	C	-	-	
OPPEE5705	-	-	-	-	A	-	G	-	G	-	-	-	-	-	-	-	A	-	T	C	-	
KR791646	-	-	-	-	A	-	G	-	G	-	-	-	-	-	-	-	A	-	T	C	-	III
PHP16-0493	-	-	-	-	A	-	G	-	G	C	-	-	-	-	-	-	A	-	C	-	-	
GMGMA1097	-	-	-	-	A	-	G	-	G	C	-	-	-	-	-	-	A	-	C	-	-	
KR792963	-	-	-	-	A	-	G	-	G	C	-	-	-	-	-	-	A	-	C	-	-	
GMGMA1095	-	-	-	-	A	-	G	-	G	C	-	-	-	-	-	-	A	-	C	-	-	
PFU-9	-	-	A	-	A	A	-	G	-	C	G	-	A	-	-	G	A	G	T	-	-	IV
PSC-10	T	A	-	-	A	-	-	G	-	-	G	-	-	-	T	-	A	-	T	-	-	V

Fig. 4. *Cox1* polymorphic sites within a 561 bp alignment of the *P. fulvicornis*-Group. Vertical numbers indicate the position of the segregation site in the alignment. Of 561 sites 539 were invariable, 10 singleton variable, and 12 parsimony informative sites. At position 543 of the alignment were three mutations, and replacements at the positions 178 and 472 were nonsynonymous (asterisks). Specimens are arranged according to their genetic distance. The Caucasian specimen PSC-11 was divergent from *P. fulvicornis* and *P. schencki* but it was similarly distant to both. Specimens are labelled with the specimen ID, the GenBank accession number or the Barcode Identification Number of the BOLD System (see supplementary Table S1). Rectangles include specimens belonging to the clades I–VI in the phylogenetic analysis (Fig. 5).

Western Europe, with clade I including the samples from Salamanca (RAxML: 88%; MrBayes: 0.99), and clade II including the samples from Zurich and Northern Spain (RAxML: 86%; MrBayes: 0.92). On the other hand, the seven *P. schencki* accessions from Canada, Germany and Zurich formed the well-supported monophyletic clade III (RAxML: 86%; MrBayes: 1.0). Finally, the three Caucasian specimens (one attributed morphologically to *P. fulvicornis* and the others to *P. schencki*) represented isolated branches (clades IV, V, and VI) whose relationships with one another and with Central European specimens remained unresolved.

Review of museum and private collections

No *P. fulvicornis* were found among *P. schencki* accessions in Swiss museums and private collections. A total of 221 museum and eight specimens from private collections could be reviewed, of which 98% had an indication of the sampling site on the label (see Appendix). All major Swiss museum and private collections harbouring *P. schencki* could be visited apart from the Naturmuseum Luzern, which has three specimens that were not accessible for visitors in February 2018. The Bündner Naturmuseum, Muséum

d’histoire naturelle Neuchâtel, Musée de la nature de Sion, Museo cantonale di storia naturale and Naturmuseum St. Gallen did not harbour *P. schencki* accessions.

DISCUSSION

Psenulus fulvicornis new to Switzerland

Surveys of urban arthropod communities in northern temperate cities frequently reveal alien species that originate from warmer climates (e.g. Germann *et al.*, 2015; Frey *et al.*, 2016; Zanetta *et al.*, 2016). The urban heat island effect, which provides warmer temperatures in the city when compared to the rural surroundings, and, presumably, the availability of nesting sites (e.g. *Sambucus* and *Rubus* wood, and artificial nests) and feeding resources (e.g. aphids) in large allotment garden areas, could explain the finding of *P. fulvicornis* in an urban garden lot (e.g. Hall *et al.*, 2017). Similarly, in Central Europe, *P. schencki* occurs in settlement areas and gardens (Blösch, 2000). Finally, discovering new cavity-nesting hymenopterans in anthropogenic habitats such as gardens may not be surprising since nests can be easily transported by humans over distances that are far beyond the dispersal capacity of adults. However, the naturalization status of *P. fulvicornis* in Switzerland remains unclear. This inconspicuous species is relatively rarely observed throughout its distribution range and it could have simply been overlooked. Yet our review of *P. schencki* accessions in Swiss museum and private collections indicates that *P. fulvicornis* could represent a recent colonizer, with to date, only two known observations: the two females that were caught in warm lowland habitats of the Cantons of Zurich and Geneva.

Taxon identification using *cox1* sequence information

While at least females of *P. fulvicornis* and *P. schencki* can be readily identified morphologically (Fig. 3), we found that neither SNPs (Fig. 4) nor the phylogeny (Fig. 5) could consistently separate the two taxa at the large geographic scale investigated. Nevertheless, specimens sampled in Central Europe belonged either to the well supported clades II (*P. fulvicornis*) or III (*P. schencki*) and may also be separated by several diagnostic SNPs (Figs 4, 5). The existence of a such spatial pattern in *cox1* sequence divergence within and among the taxa needs, however, further corroboration.

Phylogenetic relationships within the *Psenulus fulvicornis*-Group

We found that the *P. fulvicornis*-Group formed a highly supported monophyletic branch within the Central European *Psenulus* (note, however, that our phylogeny lacked *P. chevrieri* (Tournier, 1889) and the rare *P. berlandi* de Beaumont, 1937). This result

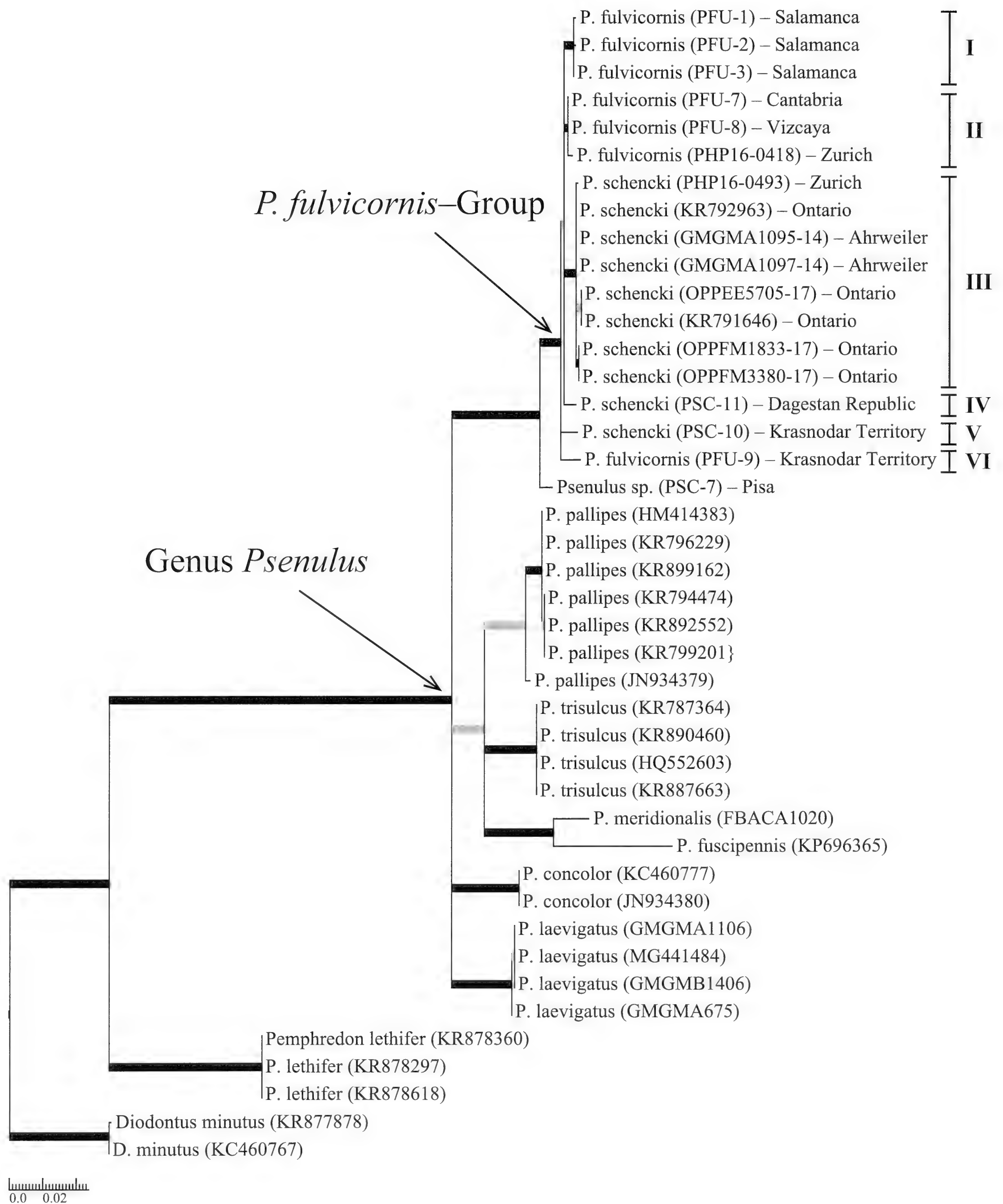


Fig. 5. Maximum likelihood tree showing the phylogenetic relationships within *Psenulus* taxa based on *cox1* and the GTR+G substitution model. All bifurcations with bootstrap values below 60% were collapsed. The bold black lines indicate bootstrap of at least 70% and the thick grey bifurcations 60-70%. Both *Diodontus minutus* (Fabricius, 1793) and *Pemphredon lethifer* (Shuckard, 1837) sequences root this tree. Specimens are labelled with the sample ID, their GenBank accession number or the Barcode Identification Number of the BOLD System, and the collection site if known (see supplementary Table S1). Six lineages I–VI were found within the *P. fulvicornis*-Group.

confirms the morphology-based hypothesis of their close relationship (Schmidt, 1971; Schmid-Egger, 2002) and is in contrast to former authors, which grouped *P. fulvicornis* with *P. fuscipennis* (Schenck, 1861; de Beaumont, 1939). However, we found polyphyly within the *P. fulvicornis*-Group, which was split in at least three well supported clades in South-Western and Central Europe. All clades were coherent with the taxonomic classification of the samples, which excludes imperfect taxonomy as a cause for polyphyly. The unresolved phylogenetic relationship between the Caucasian specimens and the South-Western and Central European clades may be interpreted as a sampling gap (i.e. incomplete sampling) in the eastern part of the distribution range of *P. fulvicornis* (Fig. 1) (Cho *et al.*, 2011; Wiens & Tiu, 2012).

Previous studies have shown that many taxa considered as valid species are polyphyletic at the *cox1* locus, especially when sampled comprehensively across (large) distribution ranges, and intra- and interspecific variability (Funk & Omland, 2003; Meyer & Pauley, 2005). Specifically, it was also found in hymenopterans (e.g. Jansen *et al.*, 2009; Nicholls *et al.*, 2012; Eimanifar *et al.*, 2018). The rather small morphological and genetic differences (Figs 2, 5) suggest that *P. fulvicornis* and *P. schencki* could be interpreted as incipient species, which are not yet reciprocally monophyletic at the *cox1* locus (i.e. incomplete lineage sorting; Funk & Omland, 2003). Similar findings have also been made in other putatively closely related Central European hymenopterans (e.g. Schmidt *et al.*, 2015). Other possible reasons for polyphyly include hybridisation and mitochondrial DNA introgression (Funk & Omland, 2003): the geographic range overlap and potentially similar habitat requirements between *P. fulvicornis* and *P. schencki* could set the stage for occasional hybridisation, and Gauss (1974) indeed observed a putative *P. fulvicornis* female *in copula* with a *P. schencki* male in South Western Germany. Yet we did not find a genetic sign of interspecific gene flow here, and, moreover, other (nuclear) loci may be more effective to detect hybrids (Petit & Excoffier, 2009; Nicholls *et al.*, 2012; Patten *et al.*, 2015; Beresford *et al.*, 2017).

CONCLUSION

We found extensive and overlapping sequence variability at the *cox1* locus between *P. fulvicornis* and *P. schencki* at the European scale. Hence, we could not identify a barcoding gap, which may hamper taxon identification. Nevertheless, in Central Europe, we found small but well supported genetic and morphological differentiation among co-occurring specimens, which corroborates their separate taxonomic treatment, consents identification and confirms *P. fulvicornis* as a new element of the Swiss hymenopteran fauna.

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APPENDIX

Museum and private collection material examined

Ambiguous information or barely readable text on a label is given in square brackets.

Psenulus fulvicornis Schenck, 1857

1 female; Avusy, Moulin de la Grave (CH: GE); 12.06.2005; leg. & det. H. Boillat; R. Neumeyer conf.; MHNG coll.

Psenulus schencki Tournier, 1889

1 female; Brusio (CH: GE); 31.07.1935 - 05.08.1935; A. Nadig leg.; M. Hermann det.; ETHZ coll. – 1 male; Pfynwald (CH: VS); 24.05.3[5]; J. de Beaumont det. 1936; ETHZ (Schulthess) coll. – 1 female; CH: VS; J. de Beaumont det. 1936; ETHZ (Schulthess) coll. – 1 male; Ardez (CH: GR); 22.06.1921; A. Breitenstein det. 2002; ETHZ coll. – 1 female; Zerne (CH: GR); 08.08.1935; A. Nadig leg.; S. Bieri det. 1996; ETHZ coll. – 1 female & 1 male; Winterthur, Töss, Rosenau (CH: ZH); 05.06.1971; A. Krebs leg. & det.; ETHZ coll. – 6 males; Winterthur, Töss, Chrugeler (CH: ZH); 09-10.02.1972; A. Krebs leg. & det.; ETHZ coll. – 3 males; Unterstammheim (CH: ZH); 02-06.04.1972; A. Krebs leg. & det.; ETHZ coll. – 1 male & 1 female; Flaach (CH: ZH); 20-25.03.1973; A. Krebs leg. & det.; ETHZ coll. – 1 male; Winterthur (CH: ZH); 19.06.1973; A. Krebs leg. & det.; ETHZ coll. – 1 female; Winterthur (CH: ZH); 26.06.1973; A. Krebs leg. & det.; ETHZ coll. – 1 female; Winterthur (CH: ZH); 04.07.1973; A. Krebs leg. & det.; ETHZ coll. – 1 female; Winterthur (CH: ZH); 11.02.1974; A. Krebs leg. & det.; ETHZ coll. – 2 females; Dielsdorf (CH: ZH); A. Krebs leg. & det.; ETHZ coll. – 1 females & 3 males; Winterthur (CH: ZH); 10-15.03.1974; A. Krebs leg. & det.; ETHZ coll. – 1 female; Flaach (CH: ZH); 27.03.1974; A. Krebs leg. & det.; ETHZ coll. – 3 females & 3 males; Nürensdorf (CH: ZH); 15-17.04.1975; A. Krebs leg. & det.; ETHZ coll. – 1 male; Eglisau (CH: ZH); 16.04.1975; A. Krebs leg. & det.; ETHZ coll. – 2 females; Kleinandelfingen

(CH: ZH); 20.04.1975; A. Krebs leg. & det.; ETHZ coll. – 6 females; CH: GR; 2-27.06.1975; A. Krebs leg. & det.; ETHZ coll. – 8 females; Uerschhausen (CH: TG); 25-26.02.1976; A. Krebs leg. & det.; ETHZ coll. – 4 females & 2 males; CH: GR; 11-14.06.1976; A. Krebs leg. & det.; ETHZ coll. – 1 female; Randen (CH: SH); 28.07.1992; 800 m a.s.l.; H. Bernasconi leg. & det.; ETHZ coll. – 2 males; Rickenbach (CH: SO); 23.06.1994; F. Amiet leg. & det.; ETHZ coll. – 1 female; Rickenbach (CH: SO); 07.07.1994; F. Amiet leg. & det.; ETHZ coll. – 1 female; city of Zurich, Zürichberg (CH: ZH); 30.05.1995; S. Ungricht leg. & det.; ETHZ coll. – 1 male; city of Zurich, Zürichberg (CH: ZH); 28.06.1995; S. Ungricht leg. & det.; ETHZ coll. – 1 male; San Vittore (CH: GR); 320 m a.s.l.; 08.04.1997; A. Salvioni leg. & det.; ETHZ coll. – 1 male; San Vittore (CH: GR); 320 m a.s.l.; 13.07.1997; A. Salvioni leg. & det.; ETHZ coll. – 1 female; Neunform, Fahrhof (CH: TG); 47.59460°N, 8.75661°E; 25.05.2012; M. Herrmann leg. & det.; ETHZ coll. – 1 female; city of Berne, Kirchenfeld (CH: BE); 12.07.1925; T. Steck leg., J. de Beaumont det. 1944; MZL coll.; GBIFCH00502859. – 1 female; city of Berne, Kirchenfeld (CH: BE); 13.08.1925; T. Steck leg., J. de Beaumont det. 1944; MZL coll.; GBIFCH00502864. – 1 female; city of Berne, Kirchenfeld (CH: BE); 13.08.1925; T. Steck leg., J. de Beaumont det. 1944; MZL coll.; GBIFCH00502856. – 1 female; city of Berne, Kirchenfeld (CH: BE); 21.08.1925; T. Steck leg., J. de Beaumont det. 1944; MZL coll.; GBIFCH00502860. – 1 female; city of Berne, Kirchenfeld (CH: BE); 31.07.1927; T. Steck leg., J. de Beaumont det. 1944; MZL coll.; GBIFCH00502858. – 1 female; Cologny (CH: GE); 30.06.1931; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502872. – 1 female; Peney (CH: GE); 05.07.1931; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502871. – 1 female; Cologny (CH: GE); 20.09.1931; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502873. – 1 female; Peney (CH: GE); 20.05.1932; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502870. – 1 male; Cologny (CH: GE); 26.06.1932; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502886. – 1 male; Cologny (CH: GE); 26.06.1932; J. de Beaumont leg. &

det.; MZL coll.; GBIFCH00502887. – 1 male; Cologny (CH: GE); 11.06.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502875. – 1 male; Cologny (CH: GE); 11.06.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502888. – 1 male; Cologny (CH: GE); 16.06.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502881. – 1 male; Cologny (CH: GE); 30.06.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502880. – 1 male; Cologny (CH: GE); 30.06.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502883. – 1 male; Cologny (CH: GE); 01.07.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502882. – 1 male; Cologny (CH: GE); 01.07.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502885. – 1 male; Cologny (CH: GE); 01.07.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502889. – 1 female; Versoix (CH: GE); 05.08.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502867. – 1 female; Allondon (CH: GE); 19.08.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502869. – 1 female; Cologny (CH: GE); 01.10.1933; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502874. – 1 female; Thun (CH: BE); 04.08.1937; Naef leg.; J. de Beaumont det.; MZL coll.; GBIFCH00502865. – 1 male; Grimentz (CH: VS); 27.07.1944-12.08.1944; J. de Beaumont leg.; J. de Beaumont det. 1957; MZL coll.; GBIFCH00502879. – 1 female; Grimentz (CH: VS); 24.06.1949-08.07.1949; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502861. – 1 female; city of Lausanne, Vidy (CH: VD); 23.07.1955; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502866. – 1 male; Losone (CH: TI); 30.06.1959-02.07.1959; J. de Beaumont leg. & det.; GBIFCH00502878. – 1 male; Gordola (CH: TI); 01.07.1959; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502877. – 1 male; Pampigny (CH: VD); 22.06.1960; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502876. – 1 male; Ecublens (CH: VD); 18.07.1962; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502884. – 1 female; La Sarraz (CH: VD); 04.08.1963; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502862. – 1 female; La Sauge (CH: VD); 16.08.1963; J. de Beaumont leg. & det.; MZL coll.; GBIFCH00502863. – 1 female; P. [Peney-le-Jorat (CH: VD)]; 02.06.1878; leg. & det. H. Tournier; MHNG coll. (Typus!). – 1 female; P. [Peney-le-Jorat (CH: VD)]; 21.06.1878; leg. & det. H. Tournier; MHNG coll. (Typus!). – 1 female; P. [Peney-le-Jorat (CH: VD)]; 05.05.1884; leg. & det. H. Tournier; MHNG coll. – 1 female; P. [Peney-le-Jorat (CH: VD)]; 05.06.1889; leg. & det. H. Tournier; MHNG coll. – 1 female; Pen. [Peney-le-Jorat (CH: VD)]; 23.05.1890; leg. & det. H. Tournier; MHNG coll. – 1 female; Nyon (CH: VD); leg. & det. H. Tournier; MHNG coll. – 1 female; Allondon (CH: GE); 16.08.1995; H. Boillat leg. & det.; MHNG coll. – 1 female; Sézegnin (CH: GE); 06.07.1997; H. Boillat leg. & det.; MHNG coll. – 1 female; Biasca (CH: TI); B. Merz leg.; A. Salvioni det.; 360 m a.s.l.; 08.07.1997; MHNG coll. – 1 female; Biel-Benken (CH: BL); 360 m a.s.l.; 30-31.05.1998; B. Merz leg.; H. Boillat det. 2006; MHNG coll. – 1 male; Leuk, Brentjong (CH: VS); 920 m a.s.l.; 15.05.2000; B. Merz leg.; H. Boillat det.; MHNG coll. – 1 male; Jussy, Les Prés de Villette (CH: GE); 475 m a.s.l.; B. Merz & Bächli leg.; H. Boillat det.; MHNG coll. – 1 female; Avusy, Moulin de la Grave (CH: GE); 22.07.2005; H. Boillat leg.; H. Boillat det. 2006; MHNG coll. – 1 female; Avusy, Moulin de la Grave (CH: GE); 10.08.2005; H. Boillat leg.; H. Boillat det. 2006; MHNG coll. – 1 male; CH: BE; 13.07.1891; T. Steck leg. & det.; NMB coll. – 1 female; Bätterkinden (CH: BE); 13.08.1892; T. Steck leg. & det.; NMB coll. – 1 female; CH: BE; 21.08.1896; T. Steck leg. & det.; NMB coll. – 1

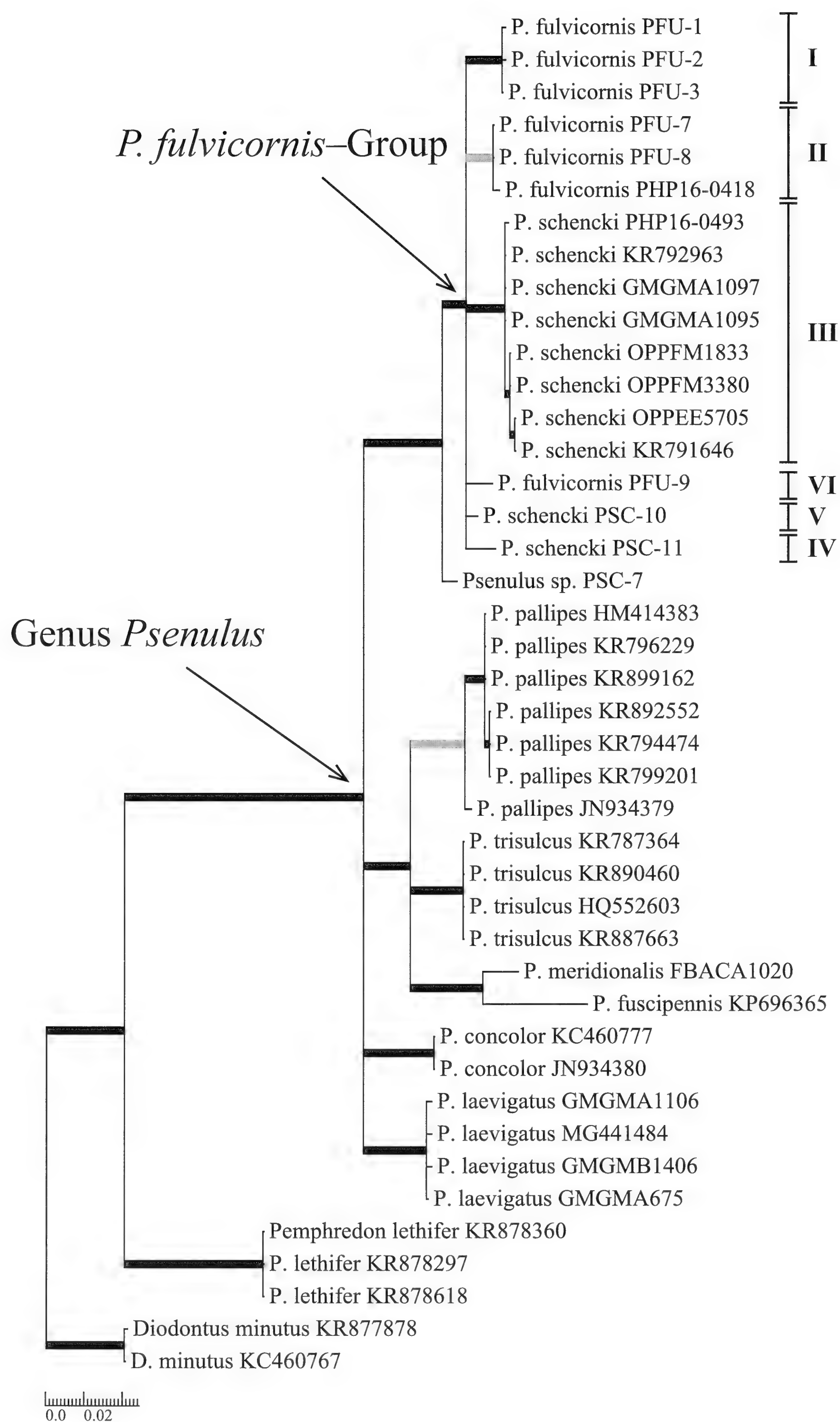
female; Unterbäch (CH: VS); 12.06.1915; T. Steck leg. & det.; NMB coll. 1 male; Unterbäch (CH: VS); 19.06.1915; T. Steck leg. & det.; NMB coll. – 1 female; city of Berne, Kirchenfeld (CH: BE); 16.08.1915; T. Steck leg. & det.; NMB coll. – 6 females; city of Berne, Kirchenfeld (CH: BE); 23.06.1918-26.09.1918; T. Steck leg. & det.; NMB coll. – 1 female; Berne, Kirchenfeld (CH: BE); [07?].06.1920; T. Steck leg. & det.; NMB coll. – 2 females; Berne, Kirchenfeld (CH: BE); 12.08.1920-16.10.1920; T. Steck leg. & det.; NMB coll. – 6 males; Lyss (CH: BE); 26.05.1921; T. Steck leg. & det.; NMB coll. – 17 females and 5 males; Kirchenfeld (CH: BE); 11.06.1921-15.09.1921; T. Steck leg. & det.; NMB coll. – 1 male; Ayent (CH: VS); 25.06.19[21?]; T. Steck leg. & det.; NMB coll. – 2 females; Kirchenfeld (CH: BE); 12.06.1922-14.06.1922; T. Steck leg. & det.; NMB coll. – 1 female; Euseigne (CH: VS); 06.08.1922; T. Steck leg. & det.; NMB coll. – 4 females and 1 male; Kirchenfeld (CH: BE); 10.06.1924-09.09.1924; T. Steck leg. & det.; NMB coll. – 31 females and 1 male; Kirchenfeld (CH: BE); 10.06.1925-21.09.1925; T. Steck leg. & det.; NMB coll. – 4 females and 1 male; 11.07.1926-24.09.1926; T. Steck leg. & det.; NMB coll. – 2 females; Kirchenfeld (CH: BE); 30.05.1927-28.06.1927; T. Steck leg. & det.; NMB coll. – 1 female; Gümligen (CH: BE); 21.06.1927; T. Steck leg. & det.; NMB coll. – 1 male; Lötschental (CH: VS); 16.07.1934; T. Steck leg. & det.; NMB coll. – 1 female; Kirchenfeld (CH: BE); [22].08.19[?]; T. Steck leg. & det.; NMB coll. – 1 female; Kirchenfeld (CH: BE); 14.06.19[?]; T. Steck leg. & det.; NMB coll. – 1 female; Martigny (CH: VS); 15.06.1889; J. de Beaumont det. 193[0]; NMBE coll. – 1 female and 1 male; Mörel (CH: VS); 28.05.[19]50; Bucher leg. & det.; NMBE coll. – 1 female; Arch (CH: BE); 24.07.1987; F. Amiet leg.; F. Amiet det. 1989; NMBE coll. – 1 female; Attisholz (CH: SO); 28-29.03.1977; F. Amiet leg.; F. Amiet det. 1989; NMBE coll. – 1 female; Rickenbach (CH: SO); 04.08.1994; F. Amiet leg. & det.; NMBE coll. – 1 female; Lostorf, Mahren (CH: SO); 28.09.1995; F. Amiet leg.; F. Amiet det. 1997; NMBE coll.

Private collection material examined

1 female; Jona, Mittlere Tägernau (CH: SG); horse pasture; 47.24109°N, 8.86645°E; 475 m a.s.l.; 25.08.1999; R. Neumeyer leg. & det.; C. Schmid-Egger conf. 2012; R. Neumeyer coll. – 1 female; Trimbach, Miesernbach (CH: SO); moist herbaceous fringe (Convolvulion); 47.36540°N, 7.87152°E; 530 m a.s.l.; 04.08.2002; H. Baur & G. Artmann-Graf leg. & det.; G. Artmann-Graf coll. 1 female; Härkingen, Untere Allmend (CH: SO); mesophilous ruderal vegetation in a gravel pit (Dauco-Melilotion); 47.29499°N, 7.82467°E; 430 m a.s.l.; 11.07.2010; G. Artmann-Graf leg., det. & coll. – 1 female; Holderbank, Chrüzacher (CH: SO); herbaceous fringe at the forest margin (Trifolion medii); 47.32849°N, 7.73273°E; 660 m a.s.l.; 26.06.2014; G. Artmann-Graf leg., det. & coll. – 1 female; Vordemwald (CH: AG); in private garden on honeydew; 47.27992°N, 7.90045°E; 446 m a.s.l.; 20.06.1982; I. Salzmann leg., det. & coll. – 1 female; Vordemwald (CH: AG); in the house at the window; 47.27992°N, 7.90045°E; 446 m a.s.l.; 08.06.1983; I. Salzmann leg., det. & coll. – 1 female; Vordemwald (CH: AG); in the house at the window; 47.27992°N, 7.90045°E; 446 m a.s.l.; 08.07.1984; I. Salzmann leg., det. & coll. – 1 male; Vordemwald (CH: AG); in the house at the window; 47.27992°N, 7.90045°E; 446 m a.s.l.; 13.06.1999; I. Salzmann leg., det. & coll.

Supplementary Table S1
Collection information for sequences produced in our lab. Sequences acquired from GenBank (GB) or the Barcode of Life Data System (BOLD) are listed below.

Taxon	Voucher (DNA-ID) / Reference	GB accession number	BOLD sequence-ID
Specimens analyzed in this study			
<i>P. fulvicornis</i> (Schenck, 1857)	Salamanca, Spain, S.F. Gayubo (PFU-1)	MG872062	–
	Salamanca, Spain, S.F. Gayubo (PFU-2)	MG872063	–
	Salamanca, Spain, S.F. Gayubo (PFU-3)	MG872064	–
	Cantabria, Spain, S.F. Gayubo (PFU-7)	MG872065	–
	Vizcaya, Spain, S.F. Gayubo (PFU-8)	MG872066	–
	City of Zurich, Switzerland, D. Frey (PHP16-0418)	KY039438	–
	Krasnodar Territory, Russia, M. Mokrousov (PFU-9)	MG872072	–
<i>P. schencki</i> (Tournier, 1889)	City of Zurich, Switzerland, D. Frey (PHP16-0493)	KY039439	–
	Krasnodar Territory, Russia, M. Mokrousov (PSC-10)	MG872073	–
	Dagestan Republic, Russia, M. Mokrousov (PSC-11)	MG872074	–
<i>Psenulus</i> sp.	Pisa, Italy, L. Strumina (PSC-7)	MG872069	–
<i>Psenulus</i> species sequences extracted either from GenBank or BOLD			
<i>P. concolor</i> (Dahlbom, 1843)	Turčinavičienė <i>et al.</i> (2016)	JN934380	GBMIN8968-12
	Turčinavičienė <i>et al.</i> (2016)	KC460777	GBMIN11495-13
<i>P. fuscipennis</i> (Dahlbom, 1843)	Becker & Keller (2015)	KP696365	GBAH11915-15
<i>P. laevigatus</i> (Schenck, 1857)	Biodiversity Institute of Ontario (2018)	MG441484	RRSSC1796-15
	Biodiversity Institute of Ontario (2018)	–	GMGMA1106_14
	Biodiversity Institute of Ontario (2018)	–	GMGMA675_14
	Biodiversity Institute of Ontario (2018)	–	GMGMB1406_14
<i>P. pallipes</i> (Panzer, 1798)	Biodiversity Institute of Ontario (2010)	HM414383	BBHEC732-10
	Hebert <i>et al.</i> (2016)	KR799201	HPPPD314-13
	Hebert <i>et al.</i> (2016)	KR892552	SMTPD1227-13
	Hebert <i>et al.</i> (2016)	KR899162	SMTPI5851-14
	Hebert <i>et al.</i> (2016)	KR796229	HEJUL005-12
	Hebert <i>et al.</i> (2016)	KR794474	JSHYM764-11
	Turčinavičienė <i>et al.</i> (2016)	JN934379	GBMIN29695-13
<i>P. schencki</i> (Tournier, 1889)	Hebert <i>et al.</i> (2016)	KR791646	MBIOD104-13
	Hebert <i>et al.</i> (2016)	KR792963	MBIOE1294-13
	Biodiversity Institute of Ontario (2018)	–	GMGMA1095-14
	Biodiversity Institute of Ontario (2018)	–	GMGMA1097-14
	Biodiversity Institute of Ontario (2018)	–	OPPEE5705-17
	Biodiversity Institute of Ontario (2018)	–	OPPFM1833-17
	Biodiversity Institute of Ontario (2018)	–	OPPFM3380-179
<i>P. trisulcus</i> (Fox, 1898)	Hebert <i>et al.</i> (2016)	KR890460	PHMTX721-11
	Hebert <i>et al.</i> (2016)	KR887663	TTMHY660-11
	Hebert <i>et al.</i> (2016)	KR787364	JSHYM986-11
	Biodiversity Institute of Ontario (2010)	HQ552603	BBHYF250-10
<i>Diodontus minutus</i> (Fabricius, 1793)	Hebert <i>et al.</i> (2016)	KR877878	NGNAX5018-14
	Turčinavičienė <i>et al.</i> (2016)	KC460767	GBMIN11500-13
<i>Pemphredon lethifer</i> (Shuckard, 1837)	Hebert <i>et al.</i> (2016)	KR878360	NGAAD389-14
	Hebert <i>et al.</i> (2016)	KR878297	NGAAF255-14
	Hebert <i>et al.</i> (2016)	KR878618	NGNAN043-14



Supplementary Figure S1

Phylogenetic tree representing species of the wasp genus *Psenulus* (Kohl, 1897). Bayesian analysis was based on *cox1* sequences (201 polymorphic nucleotides out of 637 sites), including 37 *Psenulus* and five outgroup specimens [*Diodontus minutus* (Fabricius, 1793) and *Pemphredon lethifer* (Shuckard, 1837)]. The analysis was performed with the substitution model GTR+G, estimated with jModelTest 0.1.1, and run in two chains with 5 million generations each. After discarding the burn-in, 37,501 trees were sampled of a total of 100,002 trees from both chain files. Bifurcations with posterior probabilities of <0.9 were collapsed, except for branches with ambiguous Maximum Likelihood and Bayesian results (thick grey bifurcations). All thick black branches represent posterior probabilities of at least 0.99. Specimens are labelled with the specimen ID, the GenBank accession number or the Barcode Index Number BIN of the BOLD System.

On linyphiid spiders collected by Antoine Senglet on Corsica, with the description of a new species (Araneae, Linyphiidae)

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Abstract: Spiders collected by Antoine Senglet on Corsica include 26 linyphiid species, one of which, *Bolyphantes subtiliseta* sp. nov., is described as new from a male and a female. The male of *Trichoncus hirtus* Denis, 1965 is described for the first time. Three new combinations are proposed: *Improphantes huberti* (Wunderlich, 1980) comb. nov. and *Palliduphantes corsicos* (Wunderlich, 1980) comb. nov., both ex *Lepthyphantes* Menge, 1866; *P. gladiola* (Simon, 1884) comb. nov. ex *Mansuphantes* Saaristo & Tanasevitch, 1996. *Agyneta mollis* (O. Pickard-Cambridge, 1871), *Entelecara acuminata* (Wider, 1834), *Minicia marginella* (Wider, 1834) and *Trichoncus hackmani* Millidge, 1955 are reported as new for the Corsican fauna; *Agyneta mesasiatica* Tanasevitch, 2000 is new for the Corsican and for the French fauna. In addition, a new locality of *A. mesasiatica* from Italy (Toscana) is given. The type of distribution is given for each species. The linyphiid fauna of Corsica is rich, containing at least 94 species, and can be characterized as Mediterranean, with a high proportion of presumed endemics (14%).

Keywords: French fauna - Italian fauna - new combinations - new records - endemism.

INTRODUCTION

The spider fauna of Corsica is quite well known and currently includes 557 species, 88 of which are linyphiids (Canard, 1989; Lissner, 2016; Helsdingen, 2018; etc.). The large number of linyphiid species is a surprise for this small and rather arid island, nevertheless, spiders collected by Antoine Senglet in 1971 revealed another five linyphiid species new for Corsica, and one new for science.

The aim of the present paper is to list the linyphiid spiders collected by A. Senglet at different localities on Corsica, and to describe a new species and the previously unknown male of *Trichoncus hirtus* Denis, 1965.

e.g. 1.1.1.1, which refers to the number of dorsal spines on tibiae I-IV. In Micronetinae the chaetotaxy is given in a different formula, e.g., Ti I: 2-1-1-0, which means that tibia I has two dorsal spines, one pro-, one retrolateral spine, and no ventral spines (the apical spines are disregarded). The sequence of leg segment measurements is as follows: femur + patella + tibia + metatarsus + tarsus. All measurements are given in mm. All scale bars in the figures correspond to 0.1 mm, unless indicated otherwise. Figure numbers are given above the scale lines, the corresponding distance below. The range for each species is given based on its distribution records taken mostly from Helsdingen (2018) and from the World Spider Catalogue (2018).

MATERIAL AND METHODS

This paper is based on material kept at the Muséum d'histoire naturelle de Genève, Switzerland (MHNG), unless indicated otherwise. Specimens preserved in 70% ethanol were studied using a MBS-9 stereomicroscope. A Levenhuk C-800 digital camera was used for taking photos. The terminology of copulatory organs mainly follows that of Merrett (1963), Helsdingen (1965), Hormiga (2000) and Saaristo & Tanasevitch (1996). The chaetotaxy of Erigoninae is given in a formula,

Abbreviations

ARA	anterior radical apophysis
DSA	distal suprategular apophysis
E	embolus
EP	embolus proper
L	lamella characteristica
LL	lateral lobes
MD	median denticle
MM	median membrane
PH	pit hook

PMP	posterior median plate
PO	prolateral outgrowth
R	radix
RO	retrolateral outgrowth
S	stretcher
TA	terminal apophysis
TmI	position of trichobothrium on metatarsus I
WH	hook on lateral walls
ZMMU	Zoological Museum of the Moscow State University, Moscow, Russia

RESULTS

Agyneta mesasiatica Tanasevitch, 2000

Material from Corsica examined: 1 male; FRANCE, Corsica, Prunelli di Casacconi; 22.V.1971; leg. A. Senglet. – 1 male; Porte Leccia; 2.VI.1971; leg. A. Senglet. – 2 males, 3 females; Porto; 4.VI.1971; leg. A. Senglet.

Additional material examined: 1 male; ITALY, Toscana, Mt Argentato, 280-400 m a.s.l.; 13.-14.II.1980; leg. A. Focarile.

Type material examined: ZMMU; 1 male paratype of *Agyneta mesasiatica*; AZERBAIJAN, Caucasus Mts, Talysh Mts, Amburdara near Gosmalian, *Populus* and *Salix* forest along stream, litter, under stones; 10.X.1983; leg. S. Golovatch. – ZMMU; 1 male paratype of *A. mesasiatica*; Baku, Musabekov; 24.VI.1976; leg. P. Dunin.

Remarks: *Agyneta mesasiatica* was hitherto known from the Caucasus (Azerbaijan; North Osetiya, Russia), W-Kopetdagh Mts (Turkmenistan) (Tanasevitch, 2000), and from throughout Iran (Tanasevitch, 2008, 2009). The species is new for the Corsican, French and Italian faunas (see Helsdingen, 2018). Porto on Corsica is the westernmost known locality of this species. The discovery of this species in the western Mediterranean region is surprising, but a thorough comparison of the new material with type specimens and with specimens from the Near East clearly show that all are conspecific.

Range: Ancient Mediterranean.

Agyneta mollis (O. Pickard-Cambridge, 1871)

Material examined: 1 male, 2 females; FRANCE, Corsica, Chiavari; 31.V.1971; leg. A. Senglet. – 1 male, 4 females; Ste Trinité - Porto-Vecchio; 25.V.1971; leg. A. Senglet. – 1 male; Ajaccio; 1.VI.1971; leg. A. Senglet.

Remarks: The species is new for the Corsican fauna.

Range: Palaearctic-West Nearctic.

Agyneta pseudorestris Wunderlich, 1980

Material examined: 1 male, 2 females; FRANCE, Corsica, Olmo; 5.VI.1971; leg. A. Senglet. – 1 male; Casalabriva; 29.V.1971; leg. A. Senglet.

Range: Mediterranean.

Alioranus pauper (Simon, 1881)

Material examined: 1 female; FRANCE, Corsica, Corte; 2.VI.1971; leg. A. Senglet.

Range: Mediterranean.

Araeoncus humilis (Blackwall, 1841)

Material examined: 3 males; FRANCE, Corsica, Olmo; 5.VI.1971; leg. A. Senglet. – 2 females; Prunelli-di-Casacconi; 22.VI.1971; leg. A. Senglet. – 2 males, 4 females; Filitosa, Olmeto, bank of river; 16.VI.1999; leg. A. Senglet.

Range: West Palaearctic.

Bathyphantes gracilis (Blackwall, 1841)

Material examined: 2 females; FRANCE, Corsica, Porto; 4.VI.1971; leg. A. Senglet. – 1 female; Olmo; 5.VI.1971; leg. A. Senglet.

Range: Holarctic.

Bolyphantes subtiliseta sp. nov.

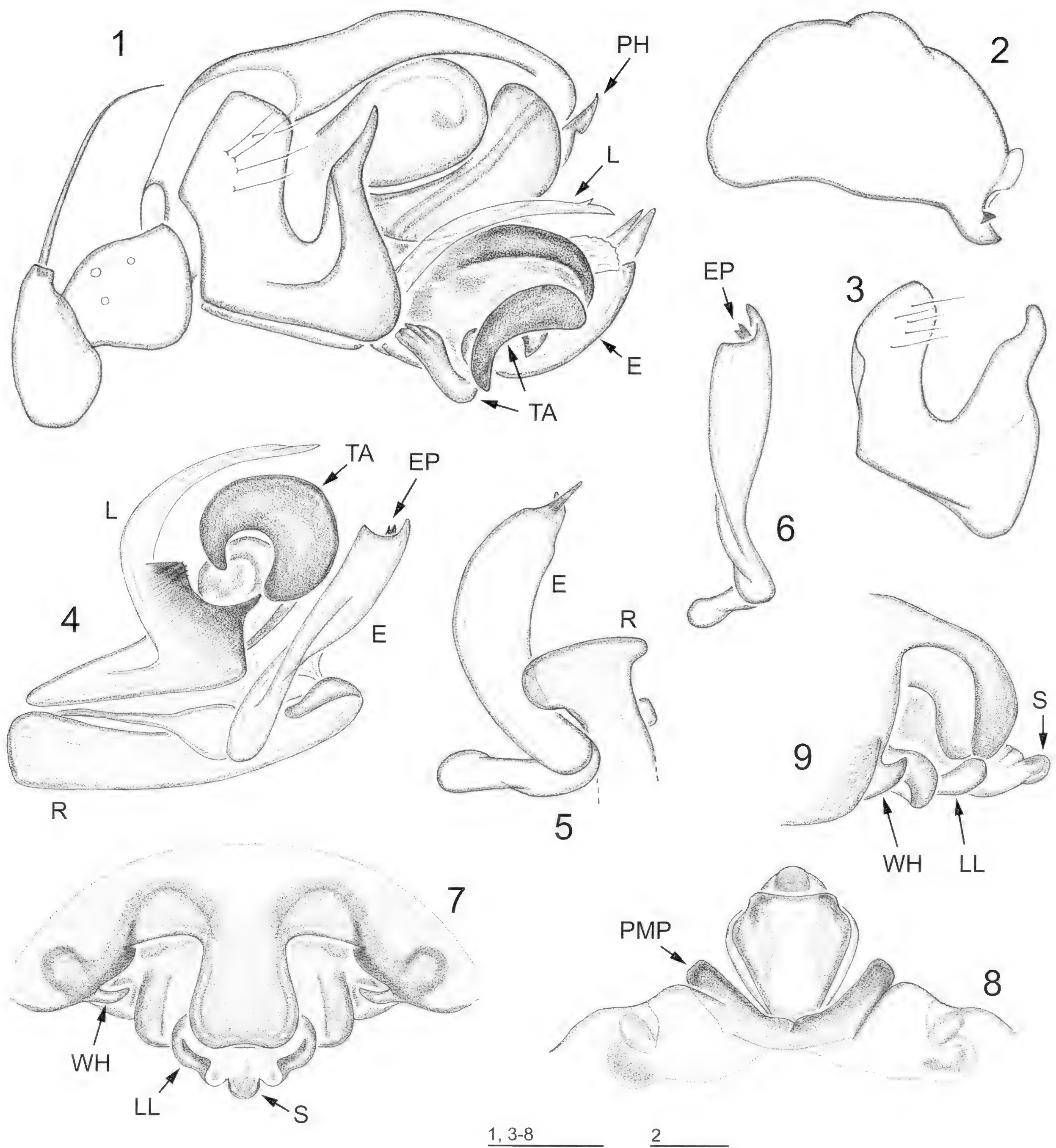
Figs 1-9

Holotype: Male; FRANCE, Corsica, Haut Asco, 1500-1700 m a.s.l.; 3.VI.1971; leg. A. Senglet.

Paratype: 1 female; collected together with the holotype.

Diagnosis: *Bolyphantes subtiliseta* sp. nov. clearly differs from all known congeners by the unarmed paracymbium and the reduced thumb on the embolus. The new species can be easily distinguished from the European representatives of the genus by a thin special seta (*sensu* Saaristo & Tanasevitch, 1996) on the palpal patella (vs. thick and serrate), by the narrow and relatively long lamella characteristic in the male, by the widely open epigynal cavity, as well as by the shape of the relatively large proscape.

Etymology: The specific epithet, a noun in apposition, is a combination of two words: “subtilis” and “seta”, referring to the shape of the special seta on the male palpal patella.



Figs 1-9. *Bolyphantes subtiliseta* sp. nov., male holotype (1-6) and female paratype (7-9). (1) Right palp, retrolateral view. (2) Cymbium, dorsal view. (3) Paracymbium, lateral view. (4) Embolic division. (5) Embolus and apex of radix. (6) Embolus. (7-9) Epigyne, ventral, dorsal and lateral view, respectively.

Description

Male holotype: Total length 2.30. Carapace unmodified, 1.10 long, 0.85 wide, pale brown. Chelicerae 0.45 long. Legs (most of them lost) pale brown. Leg I 6.58 long ($1.75+0.35+1.78+1.70+1.00$), IV: most segments lost, Fe 1.70 long. Chaetotaxy: most spines lost, see below, under description of female. Tml 0.18. Palp (Figs 1-6):

Patella with a thin, slightly curved special seta raised on a small tubercle. Tibia short, unmodified. Cymbium with almost transparent, small, posterodorsal outgrowth and claw-shaped posteroventral outgrowth with a denticle at its base. Paracymbium relatively large, toothless; all pockets strongly reduced. Lamella characteristica narrow, gradually narrowing towards tip, with a small

denticle apically. Terminal apophysis complex, massive, strongly sclerotized. Embolus narrow, elongated, slightly curved; embolus proper very short, bifid; its thumb reduced. Abdomen 1.25 long, 0.90 wide, dorsal colour pattern faded, indistinct.

Female paratype: Total length 2.70. Carapace 1.00 long, 0.75 wide. Chelicerae 0.45 long. Spines of legs mostly lost, but based on spine pores chaetotaxy formula probably TiI: 2-1-1-0, TiII: 2-0-1-0. Mt I-II: 1-0-0-0. Leg I 6.01 long (1.63+0.38+1.60+1.50+0.90), IV: most segments lost, Fe 1.63 long. TmI 0.14. Abdomen 1.88 long, 0.63 wide, dorsal colour pattern faded, indistinct. Epigyne (Figs 7-9): Lateral walls each with a hook. Proscape slightly narrowed at base, its length almost equal to its maximal width. Distal part of scape massive, lateral lobes short and wide. Stretcher strongly reduced. Posterior median plate narrow, V-shaped in ventral view. Body and leg colouration as in male.

Distribution: Known from the type locality in Corsica only.

Range: Central Mediterranean, probably endemic to the island.

***Bolyphantes nigropictus* Simon, 1884**

Material examined: 1 female; FRANCE, Corsica, Gorges de l'Ascol; 3.VI.1971; leg. A. Senglet.

Range: West Mediterranean.

***Entelecara acuminata* (Wider, 1834)**

Material examined: 1 male, 1 female; FRANCE, Corsica, Lonza; 28.V.1971; leg. A. Senglet. – 1 male, 2 females; Pont de Zipitoli, Bastelica; 30.V.1971; leg. A. Senglet. – 1 male, 1 female; Prunelli di Casacconi; 22.V.1971; leg. A. Senglet.

Remarks: The species is new for the Corsican fauna.

Range: West Palaearctic.

***Erigone dentipalpis* (Wider, 1834)**

Material examined: 2 females; FRANCE, Corsica, Olmo; 5.VI.1971; leg. A. Senglet. – 1 male, 1 female; Sotta; 27.V.1971; leg. A. Senglet. – 1 female; Chiavari; 31.V.1971; leg. A. Senglet.

Range: Holarctic.

***Gnathonarium dentatum* (Wider, 1834)**

Material examined: 4 females; FRANCE, Corsica, Ste Trinité - Porto-Vecchio; 25.V.1971; leg. A. Senglet.

Range: Palaearctic.

***Gongylidiellum murcidum* Simon, 1884**

Material examined: 1 male, 1 female; FRANCE, Corsica, Ste Trinité - Porto-Vecchio; 25.V.1971; leg. A. Senglet.

Range: Palaearctic.

***Gongylidiellum vivum* (O. Pickard-Cambridge, 1875)**

Material examined: 5 females; FRANCE, Corsica, Solenzara; 24.V.1971; leg. A. Senglet. – 1 female; Ajaccio; 1.VI.1971; leg. A. Senglet.

Range: Disjunct West Palaearctic - Far Eastern.

***Maso gallicus* Simon, 1894**

Material examined: 3 females; FRANCE, Corsica, Chiavari; 31.V.1971; leg. A. Senglet. – 1 male; Ste Trinité - Porto-Vecchio; 25.V.1971; leg. A. Senglet.

Range: West Palaearctic.

***Microctenonyx subitaneus*
(O. Pickard-Cambridge, 1875)**

Material examined: 2 females; FRANCE, Corsica, Porto; 4.VI.1971; leg. A. Senglet. – 1 female; Corsica, Olmo; 5.VI.1971; leg. A. Senglet.

Range: European-Ancient Mediterranean.

***Minicia marginella* (Wider, 1834)**

Material examined: 1 male; FRANCE, Corsica, Pont de Zipitoli, Bastelica; 30.V.1971; leg. A. Senglet.

Remarks: The species is new for the Corsican fauna.

Range: Palaearctic.

***Palliduphantes angustiformis* (Simon, 1884)**

Material examined: 1 male; FRANCE, Corsica, Satta; 27.V.1971; leg. A. Senglet. – 1 male; Col de la Testa; 27.V.1971; leg. A. Senglet. – 1 male; Pont d'Acorane, Sartène; 28.V.1971; leg. A. Senglet. – 2 females; Propriano; 29.V.1971; leg. A. Senglet. – 1 male, 1 female; Pont de Zipitoli, Bastelica; 30.V.1971; leg. A. Senglet. – 1 female; Gorges de l'Asco; 3.VI.1971; leg. A. Senglet. – 2 males, 4 females; Ajaccio; 1.VI.1971; leg. A. Senglet.

Range: Central Mediterranean.

Palliduphantes gladiola* (Simon, 1884) comb. nov.Lepthyphantes gladiola* Simon, 1884: 298.*Mansuphantes gladiola*. – Saaristo & Tanasevitch, 1996: 178.

Material examined: 3 females; FRANCE, Corsica, Prunelli-di-Casacconi; 22.VI.1971; leg. A. Senglet. – 1 female; L'Ospédale; 27.VI.1971; leg. A. Senglet. – 1 female; Zonza; 28.VI.1971; leg. A. Senglet. – 1 female; Pont de Zipitoli, Bastelica; 30.V.1971; leg. A. Senglet.

Comparative material examined: SMF #59758; 1 male, 4 females; labeled as “*Mansuphantes gladiola*; Europa: Frankreich: Corse; August [no year given]; leg. J. Wunderlich”.

Taxonomic remarks: According to the structure of the epigyne, namely, the thin and long proscape surrounded by elongated lateral walls, the strongly reduced distal part of the scape including the lateral lobes and the stretcher, this species clearly belongs to *Palliduphantes* Saaristo & Tanasevitch, 2001. Details of the male palp also support its placement in *Palliduphantes*, i.e., the shape of the embolus and of the paracymbium (see Saaristo & Tanasevitch, 2001). Thus, the allocation of *Lepthyphantes gladiola* in *Mansuphantes* Saaristo & Tanasevitch, 1996 by Saaristo & Tanasevitch (1996) should be considered as erroneous.

Range: Central Mediterranean.

***Palliduphantes longiseta* (Simon, 1884)**

Material examined: 7 males, 3 females; FRANCE, Corsica, Siaco; 20.V.1971; leg. A. Senglet. – 2 females; Propriano; 29.V.1971; leg. A. Senglet. – 1 male; Chiavari; 31.V.1971; leg. A. Senglet. – 1 male, 8 females; Haut Asco, 1500-1700 m a.s.l.; 3.VI.1971; leg. A. Senglet. – 1 female; Porto; 4.VI.1971; leg. A. Senglet.

Range: Central Mediterranean.

***Pelecopsis inedita* (O. Pickard-Cambridge, 1875)**

Material examined: 1 male; FRANCE, Corsica, Chiavari; 31.V.1971; leg. A. Senglet. – 1 male; 2 females; Ajaccio; 1.VI.1971; leg. A. Senglet.

Range: Mediterranean.

***Prinerigone vagans* (Audouin, 1826)**

Material examined: 3 females; FRANCE, Corsica, Olmo; 5.VI.1971; leg. A. Senglet.

Range: Cosmopolitan.

***Styloctetor romanus* (O. Pickard-Cambridge, 1872)**

Material examined: 1 male, 1 female; FRANCE, Corsica, Ciaco; 26.V.1971; leg. A. Senglet.

Range: Palaearctic.

***Tenuiphantes tenuis* (Blackwall, 1852)**

Material examined: 1 male; FRANCE, Corsica, Ste Trinité - Porto-Vecchio; 25.V.1971; leg. A. Senglet. – 5 males, 2 females; Propriano; 29.V.1971; leg. A. Senglet. – 2 females; Pont de Zipitoli, Bastelica; 30.V.1971; leg. A. Senglet. – 2 females; Chiavari; 31.V.1971; leg. A. Senglet. – 3 females; Ajaccio; 1.VI.1971; leg. A. Senglet. – 2 males, 2 females; Porto; 4.VI.1971; leg. A. Senglet. – 3 males, 6 females; Olmo; 5.VI.1971; leg. A. Senglet.

Range: European-Ancient Mediterranean.

***Trichoncus hackmani* Millidge, 1955**

Material examined: 1 female; FRANCE, Corsica, Ste Trinité - Porto-Vecchio; 25.V.1971; leg. A. Senglet.

Remarks: The species is new for the Corsican fauna.

Range: European-South Siberian.

***Trichoncus hirtus* Denis, 1965**

Figs 10-16

Trichoncus hirtus Denis, 1965: 436, figs 15-18 (description of female only).

Material: 1 male; FRANCE, Corsica, Sotta; 27.V.1971; leg. A. Senglet. – 1 male, 3 female; Patrimonio; 21.V.1971; leg. A. Senglet.

Remarks: This species was originally described on the basis of a single female from Bonifacio, Corsica (Denis, 1965).

Description

Male from Patrimonio: Total length 1.75. Carapace 0.80 long, 0.63 wide, unmodified, pale brown; eyes normal. Chelicerae 0.35 long, unmodified; mastidion absent. Legs pale yellow. Leg I 2.71 long (0.70+0.20+0.68+0.63+0.50), IV 2.60 long (0.75+0.22+0.63+0.60+0.40). Chaetotaxy: 1.1.1.1, length of spines about 1.5-2.5 diameters of leg segment. Metatarsi I-III with a trichobothrium. Tml 0.35. Palp (Figs 10-12): Tibia with a very long, narrow, falcate prolateral outgrowth gradually tapering towards the tip; retrolateral outgrowth conical. Cymbium with a dorsoproximal depression as typical for the genus. Distal suprategular apophysis short, tapered. Median membrane relatively wide, covering anterior apophysis of radix. Radix thin and long, its proximal part widely rounded, its distal part claw-shaped. Embolus long, forming a

loop. Abdomen 0.88 long, 0.58 wide, pale grey, sparsely covered with strong hairs dorsally.

Females from Patrimonio: Somewhat bigger than male: total length 1.80-1.91 mm. Body and leg colouration, chaetotaxy, as in male. TmI 0.36-0.37. Posterior median plate of epigyne (= dorsal plate) bent to ventral side and forming a transverse plate. Shape of this plate variable, see Figs 13-16. See also superb description of female by Denis (1965).

Taxonomic remarks: *Trichoncus hirtus* is most similar to the Eastern European *T. sordidus* Simon, 1884 and to the Western Mediterranean *T. aurantiipes* Simon, 1884, distinguished by a smaller median denticle (MD) and a pointed prolateral outgrowth on the palpal tibia, as well as by a larger, claw-shaped anterior apophysis of the radix. The main differences lie in the shape of the posterior median plate of the epigyne: large and rectangular in *T. hirtus*, almost hidden by the lateral walls in *T. sordidus*, pyramidal in *T. aurantiipes*.

Distribution: Known from Corsica only.

Range: Central Mediterranean, presumed endemic to the island.

Walckenaeria stylifrons
(O. Pickard-Cambridge, 1875)

Material examined: 1 female; FRANCE, Corsica, Prunelli-di-Casacconi; 22.VI.1971; leg. A. Senglet.

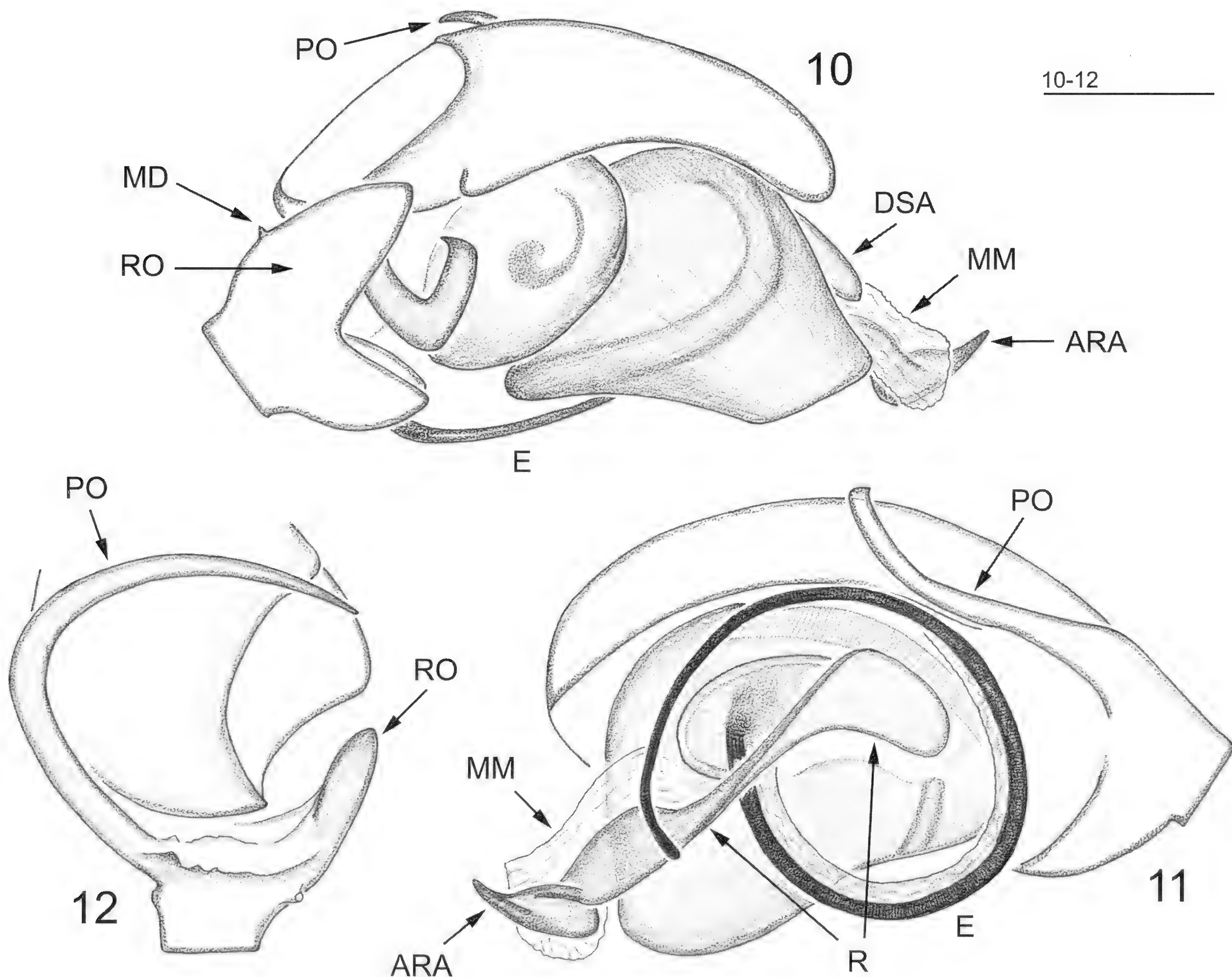
Range: European.

NOTES ON NOMENCLATURE

Improphantes huberti (Wunderlich, 1980) **comb. nov.**

Lepthyphantes huberti Wunderlich, 1980: 327, figs 25-31 (description of male and female).

Type material examined: SMF #29194; 3 male and 3 female paratypes labeled as "*Lepthyphantes huberti*



Figs 10-12. *Trichoncus hirtus* Denis, 1965, male from Patrimonio. (10-11) Right palp, retrolateral and prolateral view, respectively. (12) Palpal tibia, dorsal view.

Wunderlich; Korsika: Lac de Melo; 1976; det. und ded. Wunderlich". – SMF #34609; 1 male and 2 female paratypes labeled as "*Lepthyphantes huberti* Wunderlich; Korsika, Lac de Melo + Lac de Capitello; VII.1986; leg. und det. Wunderlich".

Taxonomic remarks: The species was original described under *Lepthyphantes* Menge, 1866 from Corsica (Wunderlich, 1980). Examining the genitalia of paratypes of both sexes showed that this species belongs to *Improphantes* Saaristo & Tanasevitch, 1996, and in its slender embolus is similar to *I. turok* Tanasevitch, 2011 (from Turkey) and to *I. cypriot* Tanasevitch, 2011 (from Cyprus).

Range: Central Mediterranean, presumed endemic to the island.

***Palliduphantes corsicos* (Wunderlich, 1980)
comb. nov.**

Lepthyphantes corsicos Wunderlich, 1980: 325, figs 18-19 (description of male only).

Type material examined: SMF #29215; male holotype labeled as "*Lepthyphantes corsicos* Wunderlich; Korsika: Lucciana; 1976; leg. Kahmann; det. Wunderlich".

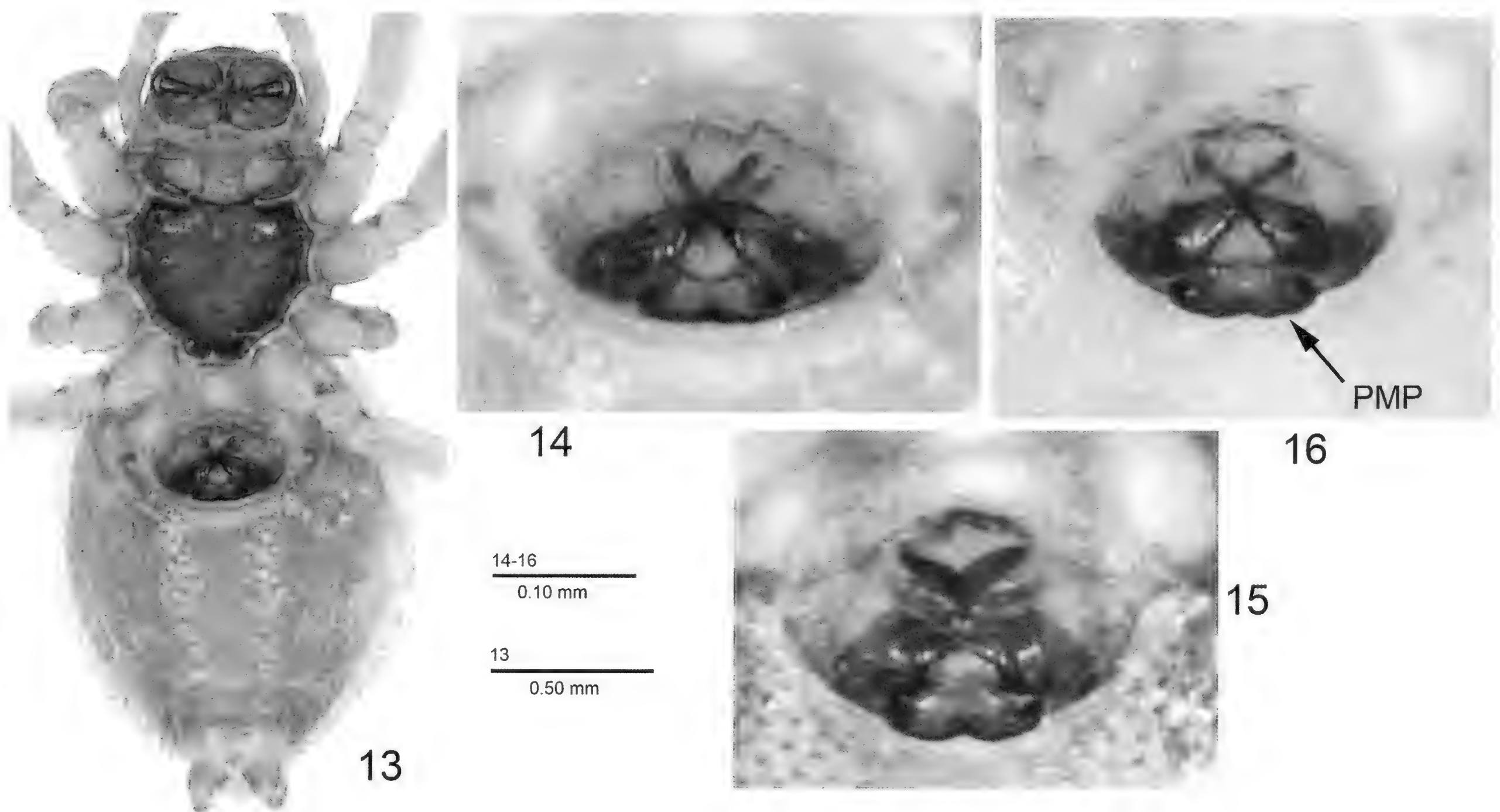
Taxonomic remarks: The species was originally described under *Lepthyphantes* from a male collected

on Corsica. My re-examination of the holotype clearly showed that the species is extremely similar to *P. gladiola* comb. nov., and like the latter, needs to be placed in *Palliduphantes*.

Range: Central Mediterranean, presumed endemic to the island of Corsica.

CONCLUSION

The Corsican linyphiid spider fauna is rich and currently known to contain at least 94 species mainly in the subfamilies Erigoninae (49 species) and Micronetinae (30 species) (Helsdingen, 2018). According to the distribution types of the species, the linyphiid fauna is typical Mediterranean and seemingly has a high level of endemism. At present there are 13 linyphiid species that are presumed to be endemic to Corsica: *Bolyphantes subtiliseta* sp. nov., *Centromerus corsicus* (Simon, 1910), *Erigonoplus inclarus* (Simon, 1881), *Hypsocephalus huberti* (Millidge, 1975), *H. nesiotes* (Simon, 1915), *Improphantes huberti* (Wunderlich, 1980) comb. nov., *Palliduphantes corsicos* (Wunderlich, 1980) comb. nov., *P. gladiola* (Simon, 1884) comb. nov., *Piniphantes cirratus* (Thaler, 1986), *Syedra nigrotibialis* Simon, 1884, *Tapinocyba corsica* (Simon, 1884), *Trichoncus hirtus* Denis, 1965 and *Typhochrestus pekkai* Bosmans & Oger, 2014. The rather high percentage of endemics (14%) clearly points out the insular character of the Corsican linyphiid fauna.



Figs 13-16. *Trichoncus hirtus* Denis, 1965, females from Patrimonio. (13) Body, ventral view. (14-16) Epigyne of three different specimens, ventral view.

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On the spider genus *Racata* Millidge, 1995, with the description of three new species (Araneae, Linyphiidae)

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Abstract: The linyphiid spider genus *Racata* Millidge, 1995 is re-diagnosed. Three species are described as new: *R. brevis* sp. nov. (male and female), *R. laxa* sp. nov. (female) and *R. sumatera* sp. nov. (male and female). The unknown female of *R. grata* Millidge, 1995 is described for the first time. The structure of the male palp of *R. grata* (the type species) is re-examined and illustrated. The taxonomic position of the genus among the linyphiid subfamilies is discussed. Most probably the genus *Racata* belongs to the subfamily Erigoninae, not to the Dubiaraneinae, and is closely related to *Aperturina* Tanasevitch, 2014b.

Keywords: Taxonomy - Erigoninae - Dubiaraneinae - Southeast Asia - Indonesia.

INTRODUCTION

The genus *Racata* Millidge, 1995 was originally described on the basis of a single male from Krakatoa Island, Indonesia, and placed in the subfamily Dubiaraneinae (Millidge, 1995). The description of the male does not contain the chaetotaxy formula, two very schematic drawings of the male palp do not reveal its detailed structure, and the absence of any corresponding females also makes the taxonomic placement of the genus unclear. New specimens of both sexes of *R. grata* from Java, Indonesia, kept at the Muséum d'histoire naturelle de Genève, Switzerland (MHNG), allowed me to re-examine the genitalia and chaetotaxy of the species. Beside that, a few other representatives of the genus from Indonesia were found in the collection of the MHNG. A re-diagnosis of the genus *Racata*, the first description of the female of *R. grata*, as well as the description of three new species from Sumatra, Indonesia, are the subject of this study.

MATERIAL AND METHODS

This paper is based on material collected in Indonesia and kept at the MHNG. Sample numbers are given in square brackets. Specimens preserved in 70% ethanol were studied using a MBS-9 stereomicroscope. A Levenhuk C-800 digital camera was used for photos. The terminology of copulatory organs mainly follows that of Merrett (1963), Millidge (1985), Hormiga (2000) and

Tanasevitch (1998, 2014b). The sequence of leg segment measurements is as follows: femur + patella + tibia + metatarsus + tarsus. All measurements are given in mm. Scale lines in the figures correspond to 0.1 mm unless indicated otherwise. Figure numbers are given above the scale lines, the alternative distance below.

Abbreviations

a.s.l.	above sea level
C	convector <i>sensu</i> Tanasevitch (1998) = plate, lamella <i>sensu</i> Millidge (1985)
D	duct
DSA	distal suprategular apophysis <i>sensu</i> Hormiga (2000)
E	embolus
MM	median membrane <i>sensu</i> Helsdingen (1965)
Mt	metatarsus
NP	national park
Re	receptacle
CD	copulatory duct
Ti	tibia
TmI	position of trichobothrium on metatarsus I

RESULTS

Racata Millidge, 1995

Type species: *Racata grata* Millidge, 1995, by original designation and monotypy.

Diagnosis: Members of the genus *Racata* can be easily recognised by the “micronetine”-like chaetotaxy, by the highly developed convector and by the presence of a panicle-shaped median membrane in the palpal organ. Females are distinguished by a distinct epigynal cavity, which is often surrounded by sclerotized swellings, and by mostly helical copulatory ducts.

The genus contains medium-sized spiders with a total length of 1.45-1.75, which are characterized by the following combination of somatic and genitalic characters:

- 1) Carapace unmodified in both sexes, eyes somewhat enlarged, cephalic pits (= sulci) absent.
- 2) Chaetotaxy formula: TiI: 2-1-1-0; II: 2-0-1-0, III-IV: 2-0-0-0; MtI-IV without spines; MtIV without trichobothrium; TmI 0.20-0.30.
- 3) Palpal tibia simple, unmodified.
- 4) Distal part of cymbium narrowed.
- 5) Convector highly developed and sclerotized.
- 6) Median membrane panicle-shaped.
- 7) Epigyne with distinct cavity, usually surrounded by sclerotized swellings.
- 8) Copulatory ducts mostly wide, helical.

Species included: *Racata brevis* sp. nov., *R. sumatera* sp. nov. (Indonesia: Sumatra), *R. grata* Millidge, 1995 (Indonesia: Krakatoa, Java and Belitung) and *R. laxa* sp. nov. (Indonesia: Sumatra; Thailand: Ko Chang).

Taxonomic remarks: The genus *Racata* was established from a male and placed into the subfamily Dubiaraneinae (Millidge, 1995) on the basis of the structure of its embolic division. Due to the same reason Millidge (1995) also placed the following Southeast Asian genera into the Dubiaraneinae: *Kenocymbium* Millidge & Russell-Smith, 1992, *Ketambea* Millidge & Russell-Smith, 1992, *Prosoptonoides* Millidge & Russell-Smith, 1992 and *Thainetes* Millidge, 1995. The subfamily Dubiaraneinae is defined by only a single character of the vulva, i.e.: “... the seminal [= copulatory] duct of the epigynum running along the margins of a lamina, as in the Mynogleninae; in the majority of the species, the lamina is coiled into a short, almost planar helix, the axis of which is more or less perpendicular to the plane of the epigynum...” (Millidge, 1993). However, as pointed out by Millidge & Russell-Smith (1992), the epigyne in all above mentioned genera (including *Racata*) is of the linyphiine type and is quite different from that of *Dubiaranea* Mello-Leitão, 1943, the type genus of the Dubiaraneinae. At present it is premature to discuss the position of these genera in the system of subfamilies in the Linyphiidae until the subfamily Dubiaraneinae is clearly diagnosed. In the meantime I provisionally consider the genus *Racata* as belonging to the Erigoninae. The small size and erigonine-like general appearance, and the structure of the genitalia, which are similar to that of some Southeast

Asian erigonines, i.e., *Asiagone* Tanasevitch, 2014a, *Houshenzinus* Tanasevitch, 2006, *Laogone* Tanasevitch, 2014a, *Nasoonia* Locket, 1982, *Oedothorax* Bertkau in Förster & Bertkau, 1883, etc., support the preliminary inclusion of *Racata* in the Erigoninae. The only problem I see here is in the chaetotaxy formula, which is absolutely not characteristic for the subfamily, but rather for the Micronetinae or Linyphiinae.

The genus is closely related to *Aperturina* Tanasevitch, 2014b, known from Thailand and West Malaysia (Tanasevitch, 2014b).

Distribution: So far known only from Indonesia and Thailand.

Racata grata Millidge, 1995

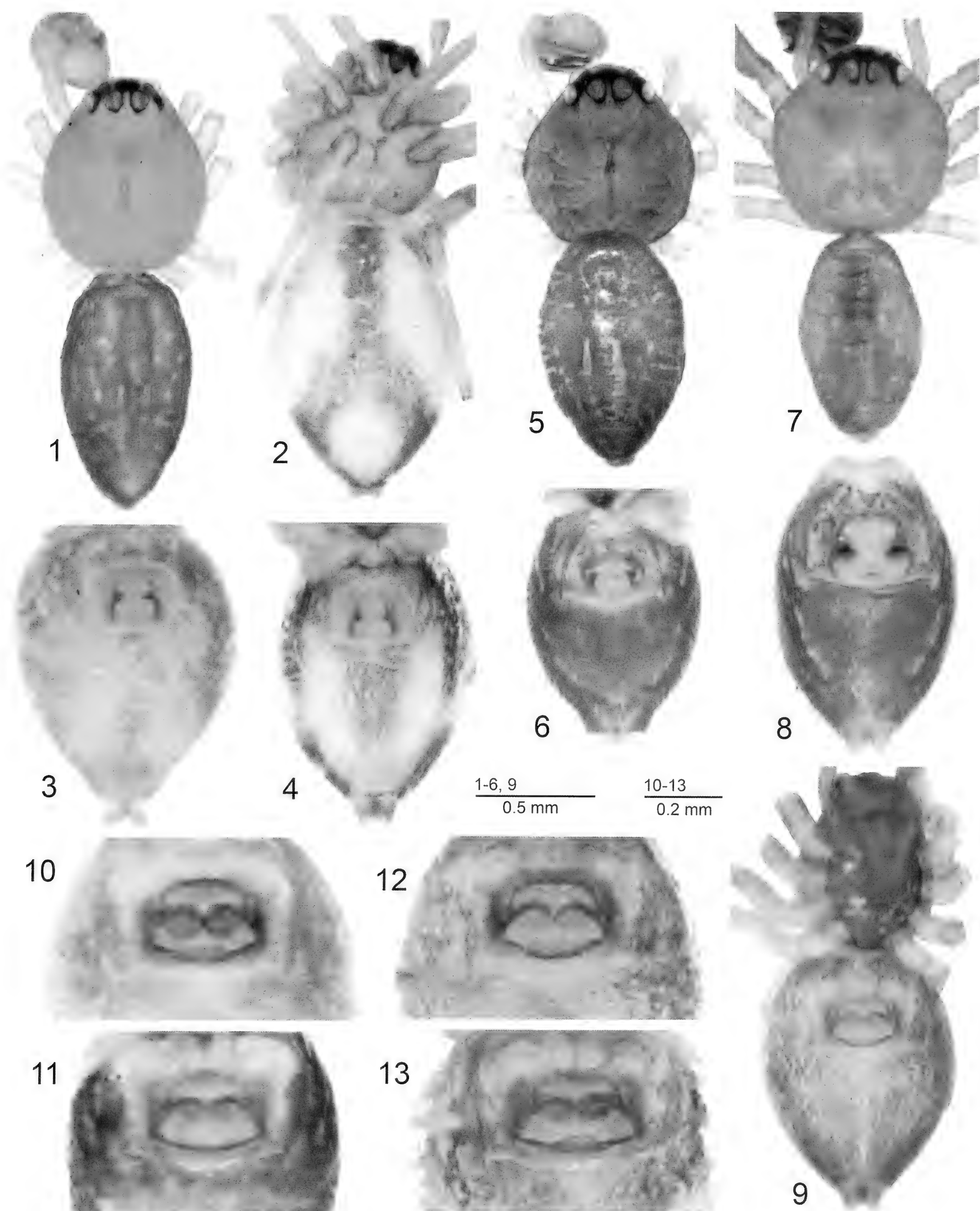
Figs 1-4, 14-15, 20, 23

Racata grata Millidge, 1995: 49, figs 62-63 (description of male).

Material examined: 1 female [Sar-87/11]; INDONESIA, Java, Bogor, Botanical Garden, soil sample between buttresses of large trees near two lakes, ca 260 m a.s.l.; 24.XI.1987; leg. B. Hauser. – 1 male [Sar-87/30]; Botanical Garden of Bogor, in nursery part, under flower pots and especially under paving slabs of the trail between greenhouses, 260 m a.s.l.; 28.XI.1987; leg. B. Hauser. – 5 males, 15 females [AS-05/11]; Java, Mt Gede - Pangrango NP, near Cibodas, 6°47'0"S, 107°01'0"E, 1450-1600 m a.s.l.; 4.-11.V.2005; leg. A. Schulz. – 1 female [IND-08/02], Belitung Island, Mt Tajam, near Gurok Beraye Waterfall, 2°47'01"S 107°51'47"E, primary forest, 150 m a.s.l.; 20.IX.2008; leg. P. Schwendinger. All new localities.

Remarks: The male holotype of *R. grata* (not examined) was described by Millidge (1995). A re-description of the male and the first description of the female are given below.

Description: *Male from near Cibodas.* Total length 1.50. Carapace unmodified, as shown in Fig. 1, 0.65 long, 0.60 wide, pale reddish brown. Chelicerae 0.30 long, mastidion absent. Chaetotaxy: TiI: 2-1-1-0; II: 2-0-1-0, III-IV: 2-0-0-0; MtI-IV without spines. Length of spines 1.5-2 diameters of corresponding leg segment. TmI 0.29. Palp (Figs 14-15, 20): Tibia short, simple. Distal half of cymbium narrowed. Narrow distal part of paracymbium longer than shown in original description (see Millidge, 1995: fig. 62 cf. Fig. 14). Distal suprategular apophysis, called tegular apophysis by Millidge (1995), large, claw-shaped. Median membrane, not mentioned in original description, panicle-shaped. Convector (called radical part [of embolus] in *op. cit.*), massive, forming a hook anteriorly. Embolus developed as a narrow long stripe, forming a loop, abruptly narrowing apically. Radix small, rounded. Abdomen



Figs 1-13. *Racata grata* Millidge, 1995 (1-4), *R. brevis* sp. nov., male holotype (5) and female paratype (6); *R. sumatera* sp. nov., male holotype (7) and female paratype (8); *R. laxa* sp. nov., female paratypes (9-13). (1, 5, 7) Male body, dorsal view. (2, 9) Female body, dorsal and ventral view, respectively. (3-4, 6, 8) Female abdomen, ventral view. (10-13) Epigyne, ventral view. Specimens from: near Cibodas (1-4), Mt Kerinci (5-6), Mt Sibayak (7-8), Bukittinggi (9, 12), Padangpanjang (10), Padangsidempuan (11), Taman Hutan Raya Bung Hatta (13).

0.80 long, 0.43 wide, uniformly grey (Fig. 1) or with a dorsal pattern similar to that in female (Fig. 2).

Female from near Cibodas. Total length 1.60. Carapace 0.63 long, 0.53 wide, unmodified, pale greyish yellow, with indistinct grey radial stripes and a narrow grey margin. Chelicerae 0.28 long. Legs yellow, its segments slightly darkened distally. Leg I 2.79 long (0.75+0.18+0.73+0.63+0.50), IV 2.51 long (0.70+0.15+0.63+0.60+0.43). TmI 0.34. Metatarsi IV without trichobothrium. Abdomen 0.95 long, 0.75 wide, dorsally grey, or cream-coloured with a grey pattern (Fig. 2). Epigyne (Figs 3-4, 23): Cavity slightly wider than long, with a rounded depression anterior to it. Copulatory ducts wide, helical; receptacles narrow, bent.

Taxonomic remarks: The male clearly differs from those of known congeners by the shape of its embolus: it is considerably thinner and longer than in *R. brevis* (Fig. 15 cf. Fig. 17); it is three times shorter than in *R. sumatera* (Fig. 15 cf. Fig. 19). The epigyne is similar to that of *R. brevis*, but differs by a larger depression anterior to the cavity (Figs 3-4 cf. Fig. 6), as well as by the shape of the helical copulatory ducts (Fig. 23 cf. Fig. 24).

Distribution: Known from the Indonesian islands of Krakatoa (type locality), Java and Belitung.

***Racata brevis* sp. nov.**

Figs 5-6, 16-17, 24

Holotype: Male [Sum-00/12]; INDONESIA, Sumatra, Jambi Province, Mt Kerinci, footpath to summit, NW of Kersik Tua, 1°44'12"S, 101°15'35"E, evergreen hill forest, sifting, 1800-1980 m a.s.l.; 16.II.2000; leg. P. Schwendinger.

Paratype: 1 female; collected together with the holotype.

Diagnosis: The species is characterized by possessing the widest and shortest embolus among all known congeners, as well as the shortest copulatory ducts.

Etymology: The specific epithet is a Latin adjective meaning "short" referring to the relatively short embolus of the male.

Description: *Male holotype.* Total length 1.45. Carapace 0.70 long, 0.63 wide, rounded (Fig. 5), pale greyish brown. Head part slightly elevated and protruded distad. Eyes enlarged, anterior median eyes much smaller than others. Chelicerae 0.30 long, mastidion absent. Legs pale greyish yellow, its segments slightly darkened distally. Leg I 2.60 long (0.75+0.15+0.65+0.67+0.38), IV 2.47 long (0.68+0.13+0.63+0.63+0.40). Chaetotaxy: TiI: 2-1-1-0; II: 2-0-1-0, III-IV: 2-0-0-0; MtI-IV without spines. Length of spines 1.5-2 diameters of corresponding leg segment. TmI 0.24. Metatarsi IV without

trichobothrium. Palp (Figs 16-17): Tibia short, simple. Distal half of cymbium narrowed. Proximal part of paracymbium wide, distal part L-shaped. Tegulum weakly sclerotized, light in colour. Distal suprategular apophysis very small. Median membrane panicle-shaped. Convector large, strongly sclerotized, covering base of embolus. Embolus very wide proximally, abruptly narrowing distally, its distal part relatively long and narrow. Abdomen (Fig. 5) 0.85 long, 0.53 wide, grey.

Female. Total length 1.50. Carapace 0.60 long, 0.50 wide, unmodified, pale greyish yellow. Chelicerae 0.25 long. Legs yellow, its segments darkened distally. Leg I 2.67 long (0.70+0.18+0.68+0.63+0.48), IV 2.24 long (0.65+0.18+0.60+0.43+0.38). Chaetotaxy as in male. Length of spines 2-2.5 diameters of corresponding leg segment. TmI 0.26. Metatarsi IV without trichobothrium. Abdomen 0.85 long, 0.63 wide, grey. Epigyne (Figs 6, 24): Cavity relatively small, depression anterior to it narrow. Copulatory ducts very wide, forming half a loop. Receptacles curved, beanlike.

Taxonomic remarks: The male can be easily distinguished by its boat-shaped convector and by the bent, thick embolus with a narrow, rapier-like distal part. The epigyne of *R. brevis* slightly resembles that of *R. grata*, but the depression anterior to the cavity is narrow instead of rounded, almost the same size as the cavity (Fig. 6 cf. Figs 3-4).

Distribution: Known only from the type locality on the densely forested southern slopes of the highest mountain of Sumatra, Indonesia.

***Racata sumatera* sp. nov.**

Figs 7-8, 18-19, 21-22, 25

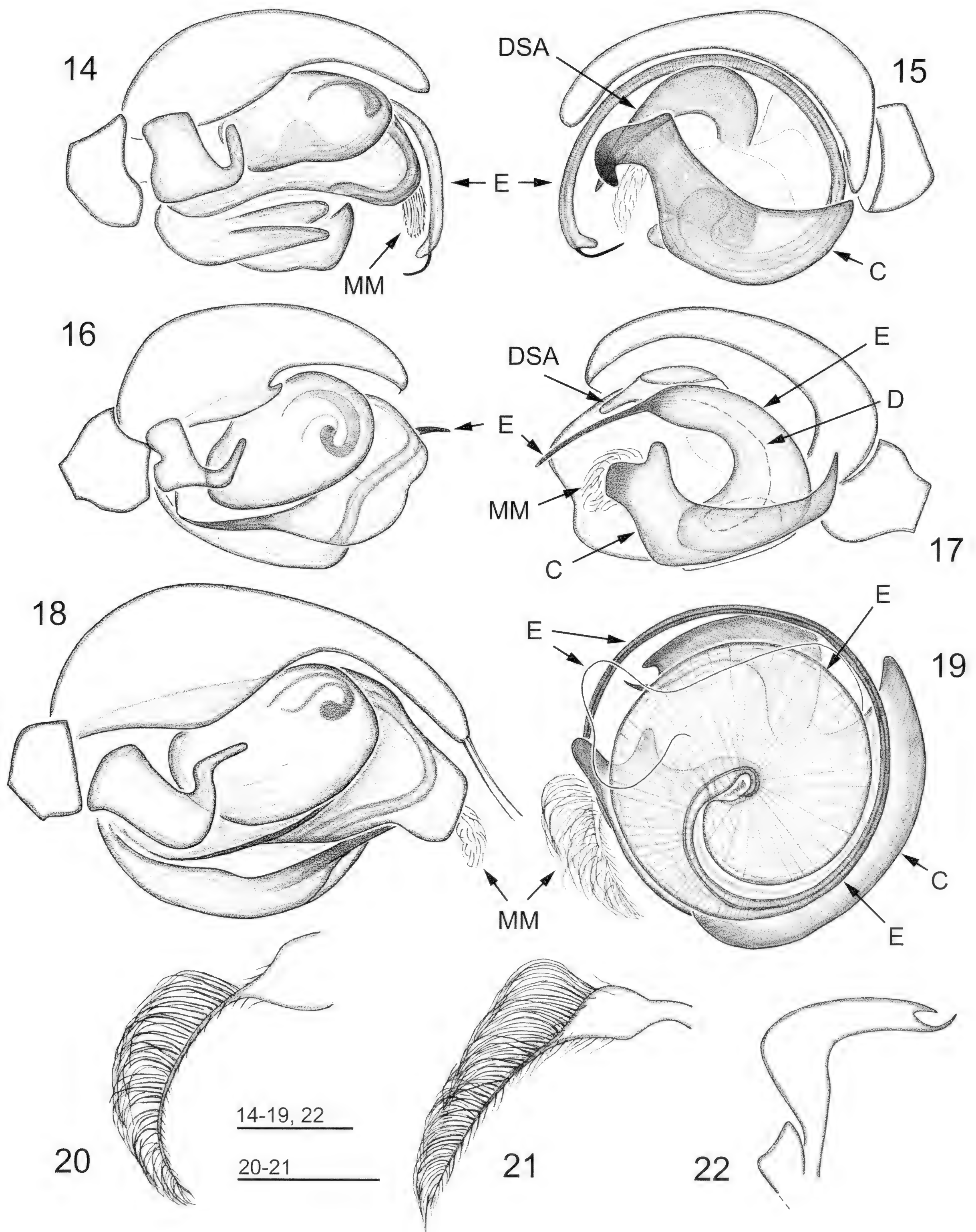
Holotype: Male [Sum-06/33]; INDONESIA, Sumatra, North Sumatra Province, Mt Sibayak, 4 km N of Brastagi, 3°13'16"N, 98°29'50"E, primary forest, 1600-1650 m a.s.l.; 6.-7.VII.2006; leg. P. Schwendinger.

Paratypes: 3 females, collected together with the holotype.

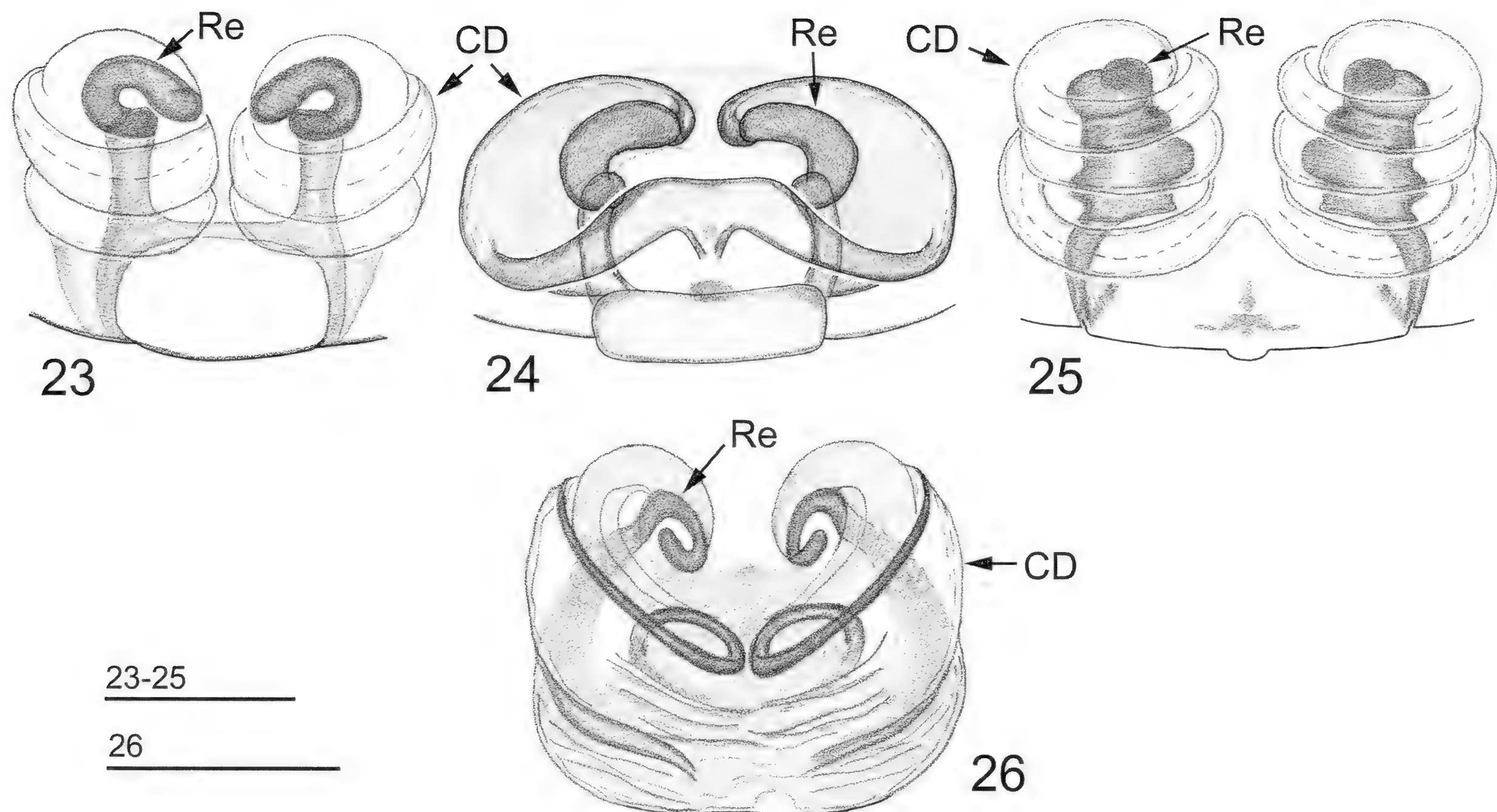
Diagnosis: The male can be easily distinguished from those of all known congeners by its very long, helical, gradually narrowing embolus; the female can be recognized by the wide anterior part of their epigyne, which is surrounded by slightly sclerotized swellings.

Etymology: The specific epithet is a name in apposition referring to the "terra typica"; "Sumatera" is the Indonesian name for "Sumatra".

Description: *Male (holotype).* Total length 1.75. Carapace 0.85 long, 0.75 wide, rounded as shown in Fig. 7, greyish yellow, with a narrow dark margin. Head part slightly elevated and protruded distad. Clypeus



Figs 14-22. Details of male palp structure of *Racata grata* Millidge, 1995, specimen from near Cibodas (14-15, 20); *R. brevis* sp. nov., holotype from Mt Kerinci (16-17); *R. sumatera* sp. nov., holotype from Mt Sibayak (18-19, 21-22). (14, 16, 18) Right palp, retrolateral view. (15, 17, 19) Right palp, prolateral view. (20-21) Median membrane. (22) Distal suprategular apophysis.



Figs 23-26. Vulva structure (dorsal view) of *Racata grata* Millidge, 1995, specimen from near Cibodas (23); *R. brevis* sp. nov., paratype from Mt Kerinci (24); *R. sumatera* sp. nov., paratype from Mt Sibayak (25); *R. laxa* sp. nov., paratype from Bukittinggi (26).

sparsely covered with long hairs. Eyes enlarged, anterior median eyes considerably smaller than others. Chelicerae 0.33 long, mastidion absent. Legs pale greyish yellow, its segments slightly darkened distally. Leg I 4.14 long ($1.00+0.23+1.15+1.08+0.68$), IV 3.46 long ($0.93+0.20+0.90+0.90+0.53$). Chaetotaxy: spines mostly lost, presumably as in female (see below). TmI 0.36. Metatarsi IV without trichobothrium. Palp (Figs 18-19, 21-22): Tibia short, simple. Distal part of cymbium narrowed. Proximal part of paracymbium wide, distal part narrow, S-shaped. Tegulum distinctly protruded distad, light in colour. Distal suprategular apophysis long, bifurcated apically. Median membrane panicle-shaped (Fig. 21). Convector massive, narrow, gradually curving. Embolus very long, forming three loops; very wide at base, gradually narrowing and in third loop becoming whip-shaped. Abdomen (Fig. 7) 1.00 long, 0.53 wide, grey.

Female. Total length 1.60. Carapace 0.65 long, 0.58 wide, unmodified, pale yellow, with a narrow grey margin. Chelicerae 0.25 long. Legs pale yellow, its segments darkened distally. Leg I 3.23 long ($0.85+0.18+0.85+0.80+0.55$), IV 2.98 long ($0.85+0.18+0.75+0.75+0.45$). TmI 0.31. Chaetotaxy: TiI: 2-1-1-0; II: 2-0-1-0, III-IV: 2-0-0-0; MtI-IV without spines. Length of spines 1.5-2 diameters of corresponding leg segment. TmI 0.36. Metatarsi IV without trichobothrium. Abdomen 1.00 long, 0.63 wide, grey. Epigyne (Figs 8, 25) relatively large; anterior part

of epigynal cavity surrounded by slightly sclerotized swellings. Copulatory ducts very wide, forming three loops. Receptacles small, indistinct.

Taxonomic remarks: The male clearly differs from those of all known congeners by its long embolus forming three loops, whereas in *R. grata* it forms one loop and in *R. brevis* only half a loop. The female is distinguished by its large epigynal cavity, the anterior part of which is surrounded by slightly sclerotized swellings.

Distribution: Known only from the type locality on the densely forested slopes of a volcano in northern Sumatra, Indonesia.

***Racata laxa* sp. nov.**

Figs 9-13, 26

Holotype: Female [Sum-06/05]; INDONESIA, Sumatra, West Sumatra Province, Batang Palupuh Rafflesia Sanctuary, 12 km N of Bukittinggi, $0^{\circ}14'32''\text{S}$, $100^{\circ}21'10''\text{E}$, 900-1100 m a.s.l., primary forest; 2.-3. VI.2006; leg. P. Schwendinger.

Paratypes: 5 females [Sum-06/01]; collected together with the holotype. – 3 females; West Sumatra Province, old secondary forest above Taman Hutan Raya Bung Hatta, near road from Padang to Lubuksulasih, $0^{\circ}56'45''\text{S}$, $100^{\circ}32'37''\text{E}$, 1100 m

a.s.l.; 29.-30.V.2006; leg. P. Schwendinger. – 1 female [Sum-06/03]; Anai Valley, 6 km S of Padangpanjang, 0°28'38"S, 100°21'14"E, primary forest, 500 m a.s.l.; 1.VI.2006; leg. P. Schwendinger. – 5 females [Sum-06/20]; disturbed primary forest near road from Lubuksikaping to Bonjol, ca 10 km S of Lubuksikaping, 0°03'16"N, 100°12'33"E, 500 m a.s.l.; 12.VI.2006; leg. P. Schwendinger. – 1 female; Mt Singalang (= Mt Singgalang), Anai Valley, 400-520 m a.s.l., secondary forest, leaf litter; 9.-24.VI.1994; leg. S. Djojosedharmo. – 2 females [Sum-06/22]; North Sumatra Province, Sipirok, Dolok Sipirok NP, near hot springs, about 30 km N of Padangsidempuan, 1°33'55"N, 99°17'03"E, disturbed hill forest, 1000 m a.s.l.; 16.VI.2006; leg. P. Schwendinger. – 1 female [AS-TH06/4]; THAILAND, Trat Province, Ko Chang, northern side, forest 3 km E of White Sand Beach, 50-200 m a.s.l., 12.02527°N, 102.308333°E; 7.XI.2006; leg. A. Schulz.

Etymology: The specific name is a Latin adjective, meaning “wide, spacious”, referring the large epigynal cavity.

Diagnosis: The female of the new species is characterised by the specific shape of its large epigyne, namely, by the two loops of the copulatory ducts, which are visible through the translucent bottom the epigynal cavity.

Description: *Female paratype from Anai Valley.* Total length 1.58. Carapace 0.63 long, 0.55 wide, pale yellow, with indistinct radial stripes and narrow grey margin. Chelicerae 0.25 long. Legs pale yellow, almost white. Leg I 2.74 long (0.75+0.18+0.73+0.65+0.43), IV 2.51 long (0.73+0.15+0.65+0.58+0.0). TmI 0.28. Chaetotaxy: TiI: 2-1-1-0; II: 2-0-1-0, III-IV: 2-0-0-0; MtI-IV without spines. TmI 0.36. Length of spines 1.5-2 diameters of corresponding leg segment. Metatarsi IV without trichobothrium. Abdomen 0.95 long, 0.70 wide, pale grey, almost white. Epigyne (Figs 9-13, 26) with a large cavity surrounded by a sclerotized swelling; a pair of loops of the copulatory ducts, which are visible through the translucent cavity bottom.

Variability: The shape of the epigyne is slightly variable, see Figs 10-13.

Taxonomic remarks: The species is only known by females but can be easily recognized by its very large epigynal cavity surrounded by a sclerotized swelling, and by a pair of loops of the copulatory ducts that can be seen through the translucent cavity bottom.

Distribution: Known from several localities on Sumatra, Indonesia and from a locality on an island off the coast of eastern Thailand.

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Rediscovery of Andrea's keelback, *Hebius andreae* (Ziegler & Le, 2006): First country record for Laos and phylogenetic placement

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Abstract: For more than a decade, the keelback snake *Hebius andreae* was only known from the holotype from the limestone forest in the central Truong Son (the Annamite Mountain Range) of Quang Binh Province in Vietnam. As the adult male was formaldehyde-fixed, the description was based on morphological characters only. During recent herpetological surveys in the karst forest of central Laos, opposite to the type locality of *H. andreae* on the other side of the Annamite Range, the Andrea's keelback is rediscovered. Based on a juvenile male from Bualapha District, Khammouane Province, within Hin Nam No National Protected Area, we herein report the first country record of this species from Laos, provide an expanded morphological definition, and for the first time recover the phylogenetic relationship of *H. andreae*, based on the sequences of four genes, including one mitochondrial, cytochrome b, and three nuclear markers, Cmos, NT3, and Rag1. The phylogenetic placement of *H. andreae* reveals it to be a member of *Hebius*, in fact the most basal representative of the genus. The rediscovery of the beautiful but still poorly known and obviously rare species underlines the conservation importance of the Annamite Mountain Range as habitat and refugium for the regional unique biodiversity, which only occurs in this karst massif.

Keywords: Khammouane Province - Hin Nam No National Protected Area - Natricidae - morphology - phylogeny.

INTRODUCTION

Amphiesma andreae was discovered in 2004 and officially described two years later by Ziegler & Le (2006). The original description was based on an adult male collected in the limestone forest in the central Truong Son (the Annamite Mountain Range) of Quang Binh Province in Vietnam. As the adult male individual was formaldehyde-fixed, the description was based on morphological characters only. *A. andreae* was diagnosed

as a representative of the genus *Amphiesma* because of the head being distinct from the body, the large eyes with round pupils, the anteriorly broadly truncated internasals, the laterally positioned nostrils, the keeled dorsal scales in 19 rows, the divided precloacal scute, the paired subcaudals, less than 35 maxillary teeth arranged in a continuous series with the two posteriormost enlarged, and the undivided hemipenis and sperm groove (Ziegler & Le, 2006).

A recent molecular study showed that the genus *Amphiesma* sensu lato is not monophyletic, and that there exist three distinct, monophyletic lineages, i.e., *Amphiesma* sensu stricto, *Hebius*, and *Herpetoreas* (Guo *et al.*, 2014). The genus *Amphiesma* is now monotypic (*A. stolatum*). *Herpetoreas* contains three species (*H. burbrinki*, *H. platyceps*, and *H. sieboldii*), and *Hebius* comprises the remaining species formerly listed under *Amphiesma* (*H. andreae*, *H. arquus*, *H. atemporalis*, *H. beddomei*, *H. bitaeniatus*, *H. bou-lengeri*, *H. celebicus*, *H. clerki*, *H. conelarus*, *H. craspedogaster*, *H. deschauenseei*, *H. flavifrons*, *H. frenatus*, *H. groundwateri*, *H. inas*, *H. ishigakiensis*, *H. johannis*, *H. kerinciensis*, *H. khasiensis*, *H. leucomy-stax*, *H. metusius*, *H. miyajimae*, *H. modestus*, *H. monticola*, *H. nicobariensis*, *H. octolineatus*, *H. optatus*, *H. parallelus*, *H. pealii*, *H. petersii*, *H. popei*, *H. pryeri*, *H. sanguineus*, *H. sarasinorus*, *H. sarawacensis*, *H. sauteri*, *H. taronensis*, *H. venningi*, *H. vibakari*, *H. viperinus*, and *H. xenura*), resulting in the new combination *H. andreae* (Guo *et al.*, 2014); for taxonomic authorities and the original publication of species names see Uetz *et al.* (2018) and for updated species names see Kizirian *et al.* (2018). For more than a decade, the Andrea’s keelback was only known from the holotype. In the original description (Ziegler & Le, 2006) the type locality was given as adjacent to Phong Nha - Ke Bang National Park, Thuong Hoa Commune, Minh Hoa District. Since then, the area has been included in the extension of Phong Nha – Ke Bang National Park (e.g., Ziegler *et al.*, 2010; Luu *et al.*, 2013).

During a recent herpetological survey by our team in the karst forests of the Hin Nam No National Protected Area in Khammouane Province in central Laos, just opposite to Phong Nha – Ke Bang on the other side of the Annamite Range, an individual of a keelback snake was found, showing the unique and characteristic colour pattern of *H. andreae*. Based on this juvenile individual we herein are able to report the first country record of this poorly known species for Laos, provide an expanded morphological definition, and recover the phylogenetic relationship of *H. andreae*.

MATERIAL AND METHODS

Sampling: This study is based on a newly collected *Hebius andreae*, a juvenile male, VNUF R.2017.25 (field number NM 17.25), from Nong Ma Village, Bualapha District, Khammouane Province, within Hin Nam No National Protected Area, collected by Vinh Quang Luu and Ngoan Van Ha, at an elevation of 537 m a.s.l., on 9 April 2017. The specimen was anaesthetized with ethyl acetate, fixed in approximately 85% ethanol, and then transferred to 70% ethanol for permanent storage. A tissue sample was preserved separately in 95% ethanol. The *H. andreae* from Laos was subsequently

deposited in the collection of the Vietnam National University of Forestry (VNUF), Hanoi, Vietnam. The holotype of *H. andreae* (ZFMK 83747) is deposited in the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany (see Ziegler & Le, 2006).

Morphological examination: Identification of sex was performed by inspection of presence of hemipenes (which have been tried to be everted before fixation and thus are partially protruding from the cloaca). Measurements were taken after preservation with a measuring tape. The number of ventral scales was counted according to Dowling (1951). The numbers of dorsal scale rows are given at one head length behind head, at midbody, and at one head length before vent, respectively. Due to the uniqueness and fragility of the new record from Laos and due to its small size we refrained from invertedly dissecting hemipenes as well as dissect the upper jaw for maxillary teeth count. Scalation was studied by using a binocular. We herein use the term precloacal instead of anal. Bilateral values were given as left / right. Abbreviations of morphological characters used in the text / Table 1 are as follows: – *Measures and ratios*: SVL: snout-vent length. – TaL: tail length. – TL: total length (SVL + TaL). – TaL/TL: ratio tail length/total length. – *Meristic characters*: ATem: anterior temporal scales (in contact with postocular scale / scales). – BodySc: body scales. – InN/Lor: Internasal and loreal in contact. – DSR:

Table 1. Sex, morphometry and scalation of the holotype of *Hebius andreae* from Vietnam (after Ziegler & Le, 2006) and the newly collected specimen from Laos.

	ZFMK 83747 holotype	VNUF R.2017.25
Sex	male	male
TL	608	290
SVL	420	209
TaL	188	81
TaL/TL	0.31	0.28
SL	9/9	9/9
SL/orbit	4-6	4-6
IL	9/9	9/9
PreOc	1/1	1/1
PostOc	3/3	3/3
Lor	1/1	1/1
Atem	1/1	1/1
PTem	1/1	2/2
DSR	19-19-17	19-19-17
PreVen	2	2
Ven	179	180
Prec	divided	divided
Subc	99	103

dorsal scale rows. – IL: infralabial scales. – Lor: loreal scales. – PreOc: preocular scales. – PreVen: preventral scales. – PostOc: postocular scales. – PTem: posterior temporal scales (in contact with anterior temporal scale / scales). – SL: supralabial scales. – SL/orbit: supralabial scale / scales touching the orbit. – Subc: subcaudal scales (without terminal scute). – SubOc: subocular scales. – TailSc: tail scales. – Ven: ventral scales.

Molecular analyses: Extracted DNA from the fresh tissue was amplified by PCR mastermix (Fermentas, Burlington, ON, Canada) using the same primers and conditions employed by Guo *et al.* (2014). In total, we sequenced four genes, including one mitochondrial, the cytochrome b, and three nuclear, Cmos, NT3, and Rag1, markers. PCR products were separated by electrophoresis through a 1% agarose gel (UltraPure™, Invitrogen, La Jolla, CA). Gels were stained for 10 min in 1 X TBE buffer with 2 pg/ml ethidium-bromide and visualized under UV light. Successful amplifications were purified to eliminate PCR components using a GeneJET™ PCR Purification kit (Fermentas). Purified PCR products were sent to FirstBase Malaysia for sequencing (see Table in Appendix).

The sequences were aligned in ClustalX v2 (Thompson *et al.*, 1997) with default settings. Data were analyzed using maximum parsimony (MP) and maximum likelihood (ML) as implemented in PAUP 4.0b10 (Swofford, 2001), and Bayesian analysis in MrBayes 3.2 (Ronquist *et al.*, 2012). For MP analysis, heuristic analysis was conducted with 100 random taxon addition replicates using tree-bisection and reconnection (TBR) branch swapping algorithm, with no upper limit set for the maximum number of trees saved. Bootstrap support (BP) (Felsenstein, 1985) was calculated using 1000 pseudo-replicates and 100 random taxon addition replicates. All characters were equally weighted and unordered. For ML analysis, we used the optimal evolution model as selected by ModelTest v3.7 (Posada & Crandall, 1998). To estimate BP in the ML analysis, a simple taxon addition option and 100 pseudo-replicates were employed. We assumed bootstrap values of $\geq 70\%$ to represent strong support and values of $< 70\%$ as weak support (Hillis & Bull, 1993). To verify the ML results, we also performed an analysis in IQ-TREE v1.6.7.1 (Nguyen *et al.*, 2015) using a single model, GTR+I+G, as selected by ModelTest with 10,000 ultrafast bootstrap replications.

For Bayesian analyses, we used the optimal model determined by Modeltest with parameters estimated by MrBayes 3.2.1. Two simultaneous analyses with four Markov chains (one cold and three heated) were run for 10 million generations with a random starting tree and sampled every 1000 generations. Log-likelihood scores of sample points were plotted against generation time to determine stationarity of Markov chains. Trees generated before log-likelihood scores reached

stationarity were discarded from the final analyses using the burn-in function. Two independent analyses were run simultaneously. The posterior probability (PP) values for all clades in the final majority rule consensus tree are provided. We ran analyses using both combined and partitioned datasets to examine the robustness of the tree topology (Nylander *et al.*, 2004; Brandley *et al.*, 2005). In the mixed model analysis, we partitioned the data into 12 sets based on gene codon positions (first, second, and third) of cytochrome b, cmos, NT3, and Rag1. Optimal models of molecular evolution for the partitions were calculated using Modeltest, and then assigned to these partitions in MrBayes 3.2 using the command APPLYTO. Model parameters were inferred independently for each data partition using the UNLINK command. All models employed in Bayesian analyses are shown in Table 2.

RESULTS

The juvenile male (Figs 1-4) was found during daytime actively crawling on a limestone forest path under dry leaves. The surrounding habitat was karst forest, dominated by species of Ebenaceae, Dracaenaceae, Arecaeae, Poaceae, Meliaceae, and Moraceae.

Morphological assessment

Measurements, ratios and scalation data of the new record of *Hebius andreae* from Laos compared to the holotype from Vietnam are presented in Table 1.

The newly collected specimen from Hin Nam No National Protected Area largely agreed with the description of the holotype of *H. andreae* from Phong Nha – Ke Bang National Park (see Fig. 5), except for the following deviations:

Supranasals slightly wider than long (*vs.* slightly longer than wide in the holotype). Suture between the supranasals slightly shorter than the suture between the prefrontals (*vs.* suture being slightly longer in the holotype). Two posterior temporals (*vs.* one posterior temporal in the holotype). Supralabials 8 and 9 being the largest (*vs.* the eighth being the largest in the holotype). The first 5/6 infralabials border the anterior chin-shields (*vs.* the first five infralabials in the holotype). 180 ventrals (*vs.* 179 in the holotype); 103 subcaudals (*vs.* 99 in the holotype). Dorsal scale rows keeled, with a narrow, sharp keel, except for outermost 1-2 rows; keels in part become indistinct towards the second body half; somewhat beyond midbody also outermost dorsal scale rows in part with keel (*vs.* dorsals distinctly keeled; somewhat beyond midbody also outermost dorsal scale row with distinct keel in the holotype).

From pictures of the underside of the juvenile male from Laos taken alive, it becomes obvious that the venter in the juvenile male was of cream colour in the head and neck region in life, but later turning into pinkish orange including the lower tail surface.

Table 2. Models used in Bayesian analyses.

Data set	Model determined by ModelTest
Combined Bayesian analysis	
Concatenated matrix	GTR+I+G
Partitioned Bayesian analysis	
Cytochrome b 1st position	TVM+I+G
Cytochrome b 2nd position	HKY+I+G
Cytochrome b 3rd position	TrN+I+G
Cmos 1st position	K80+I
Cmos 2nd position	HKY
Cmos 3rd position	K80
NT3 1st position	JC
NT3 2nd position	HKY+80
NT3 3rd position	TrNef+I
Rag1 1st position	HKY
Rag1 2nd position	HKY
Rag1 3rd position	HKY



Fig. 1. Portrait of the first record of *Hebius andreae* from Laos in life. Photo V. Q. Luu.



Fig. 2. General views of the juvenile male of *Hebius andreae* from Laos in life. Photos V. Q. Luu.



Fig. 3. Head views of the juvenile male of *Hebius andreae* (VNUF R.2017.25) from Laos in preservative. Photos T. Ziegler.

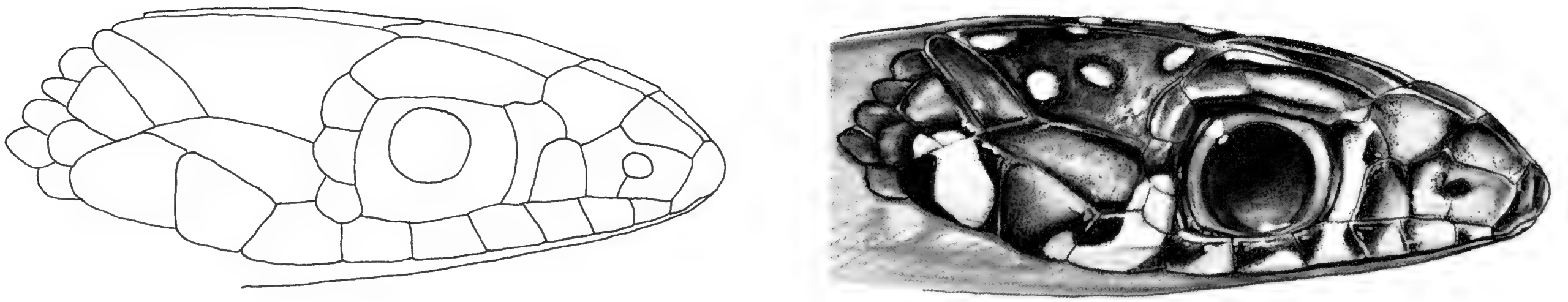


Fig. 4. Line drawing and colour painting of the right head side of *Hebius andreae* (VNUF R.2017.25) from Laos. Drawing T. Ziegler, painting C. Niggemann.

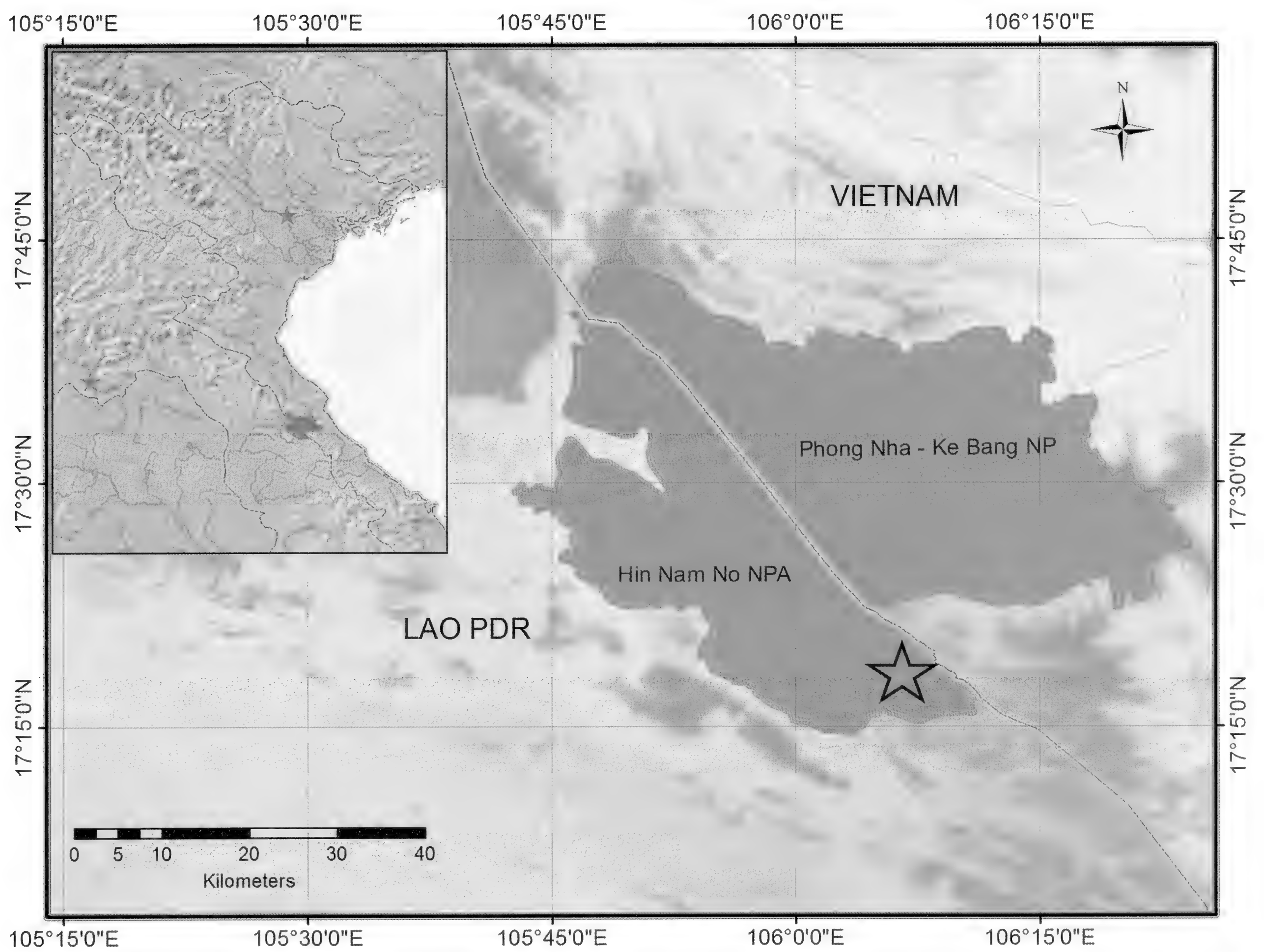


Fig. 5. Location of the Hin Nam No National Protected Area in central Laos, where the new record (star) of *Hebius andreae* took place, which is located opposite to the type locality in Vietnam, viz. Phong Nha – Ke Bang National Park in Vietnam.

Molecular results

The final matrix consisted of 3162 aligned characters, of which 503 were parsimony informative. The alignment contained no gap. MP analysis of the dataset recovered a single most parsimonious tree with 2568 steps (CI = 0.42; RI = 0.43). In the ML analysis, the -Ln likelihood score of the single best tree found was 15,553.39. The cutoff point for the burn-in function was set to 20 in combined and 21 in partitioned Bayesian analyses as -lnL scores reached stationarity after 20,000 and 21,000 generations, respectively. The topologies derived from our study are similar to those in Guo *et al.* (2014). Our phylogenetic results revealed that *H. andreae* is strongly corroborated as a member of the genus *Hebius* in all analyses (BP_{MP} = 96, all other values = 100, including the BP value derived from the ML analysis using IQ-TREE). In addition, it represents the most basal taxon of the genus (Fig. 6).

DISCUSSION

The first phylogenetic evaluation of *Hebius andreae* based on the new finding from Laos revealed it to be a member of *Hebius*. Ziegler & Le (2006) already expected

future records of *H. andreae* from Laos due to the close proximity of the type locality to the border with Laos. Unless molecular comparison with topotypic *Hebius andreae* from Phong Nha – Ke Bang shows otherwise, we assess the new record of this species from Laos for the time being as conspecific. At this stage of knowledge, the minor morphological deviations can be explained by 1) individual variation, in concert with 2) juvenile age of the individual from Laos and 3) suboptimal preservation condition. The new record from Laos also was found in the same kind of biotope, on the ground of limestone forest at a similar elevation compared with the holotype (537 m vs. 450 m).

The original diagnosis of *H. andreae* thus can be expanded as follows:

- 1) Body and tail slender, tail cylindrical and tapering; tail/total length ratio in males 0.28-0.31;
- 2) the eye diameter, if projected forward, reaches beyond the suture of first and second supralabial;
- 3) a single loreal;
- 4) a single preocular;
- 5) three postoculars;
- 6) a single anterior temporal followed by 1 or 2 posterior temporals;

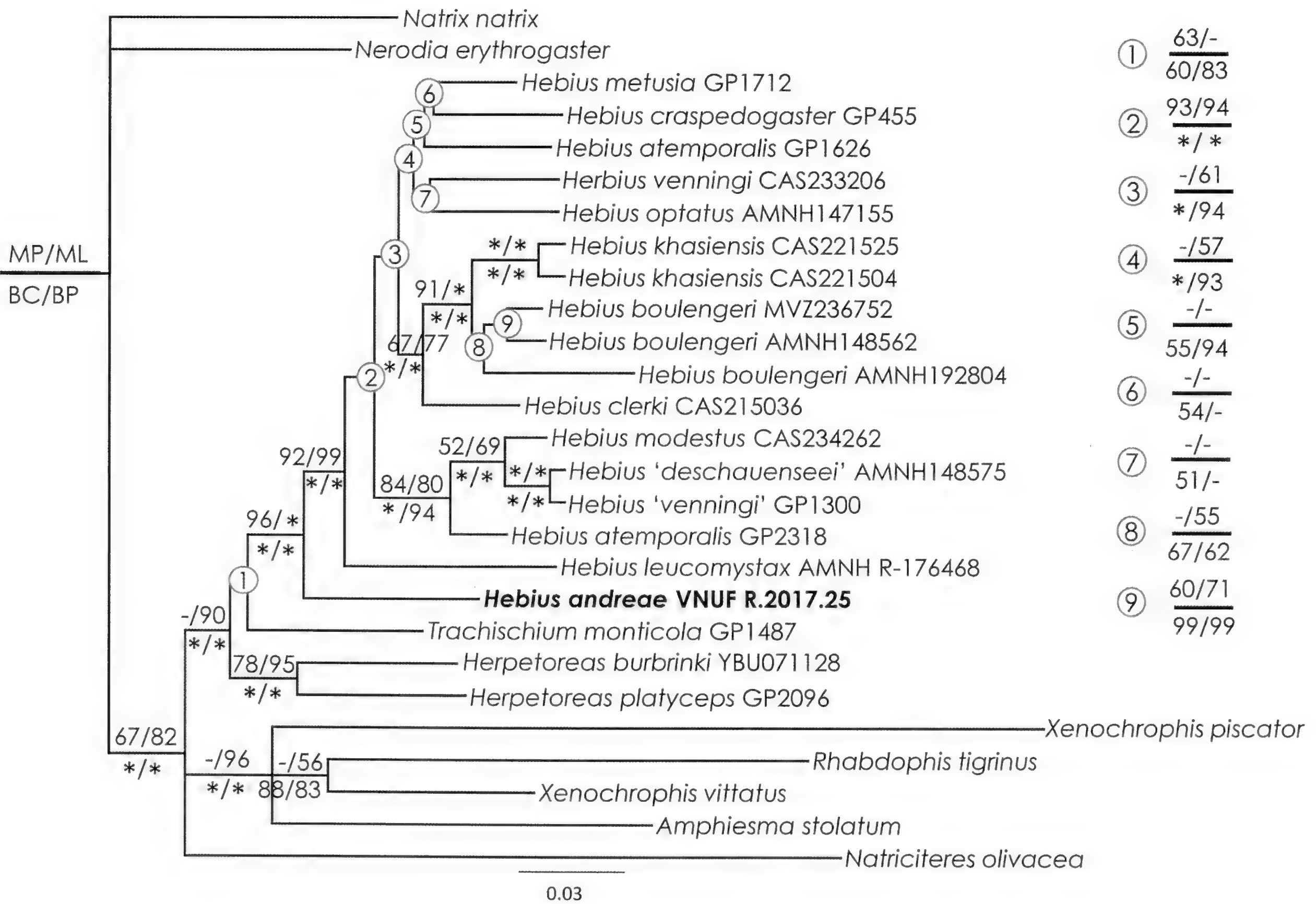


Fig. 6. Bayesian phylogram based on all data combined and a single model. Numbers above and under branches are MP/ML bootstrap values and combined/partitioned Bayesian posterior probabilities (>50%), respectively. Hyphen and asterisk denote <50% and 100% values, respectively.

- 7) nine supralabials, fourth to sixth in contact with the eye, 8th or 8th and 9th supralabials largest;
- 8) nine infralabials, first pair in contact with each other behind the mental, the first five or six bordered by the anterior chin-shields;
- 9) posterior chin-shields longer than anterior ones, separated from each other on their entire length by gular scales;
- 10) 179-180 ventrals (plus two preventrals);
- 11) precloacal plate divided;
- 12) 99-103 divided subcaudals;
- 13) dorsal scales in 19-19-17 rows, keeled, except outermost row(s) in the anterior body, with a narrow, sharp keel;
- 14) dorsal ground coloration brownish-olive, with a pale, black-edged bar before and behind the eye; head and neck with several pale, dark-edged blotches that turn into pale and black-edged transversal bars on the anterior body; such a transversal bar pattern dissolves anterior to the midbody region and then turns into a series of small pale blotches that build each a dorso-lateral stripe that ends at the dorsal tail base;
- 15) venter light, laterally with dark spots in the forebody region; cream in the anterior body, then turning into pinkish orange at least in juvenile males;
- 16) 34 maxillary teeth, arranged in a continuous series, the two posteriormost distinctly enlarged, without diastema;
- 17) hemipenis simple, with undivided sperm groove; the outer genital organ is covered with small spines except for a single, strongly enlarged spine next to the sperm groove at the hemipenis base and except for irregularly arranged medium-sized spines that encircle the hemipenis horizontally at the trunco-pedicel area.

There exist other local endemic herpetofauna representatives in Hin Nam No and Phong Nha – Ke Bang, such as the tree frog *Gracixalus quyeti* (Nguyen, Hendrix, Böhme, Vu & Ziegler, 2008), which is known only from central Vietnam's Quang Binh Province and from Khammouane Province in central Laos (Nguyen *et al.*, 2008; Egert *et al.*, 2017), or the bent-toed gecko species *Cyrtodactylus cryptus* Heidrich, Rösler, Vu, Böhme & Ziegler, 2007, which also can be found only along the Annamite Mountain Range of central Vietnam and Laos (Heidrich *et al.*, 2007; Luu *et al.*, 2016). However, Luu *et al.* (2016) also could uncover cryptic *Cyrtodactylus* speciation along both sides of the Annamites, with five endemic karst-dwelling *Cyrtodactylus* occurring in a restricted area on opposite sides of the Range. In Vietnam, there are two endemic karst-adapted species, *C. phongnhakebangensis* Ziegler, Rösler, Herrmann & Vu, 2002 and *C. roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz, 2010 as opposed to three endemic karst-adapted species in Laos, *C. calamei* Luu, Bonkowski, Nguyen, Le, Ngo, Schneider & Ziegler,

2016, *C. hinnamnoensis* Luu, Bonkowski, Nguyen, Le, Ngo, Schneider & Ziegler, 2016, and *C. sommerladi* Luu, Bonkowski, Nguyen, Le, Ngo, Schneider & Ziegler, 2016 (Ziegler *et al.*, 2002, 2010; Luu *et al.*, 2016). According to Luu *et al.* (2016), the rapid adaptation to isolated local karst conditions compared with generalist ground or tree-associated taxa might offer an explanation for such cryptic speciation processes on karst, as the environmental conditions in karst are known to accelerate evolutionary processes (Nicolas *et al.*, 2012; Le *et al.*, 2015).

The new record of the beautiful but still poorly known and rare species *H. andreae* in Laos underlines the importance of the Hin Nam No National Protected Area as habitat and refugium for the regional unique biodiversity, which only occurs in this karst massif. Phong Nha – Ke Bang already is UNESCO World Heritage Site whereas Hin Nam No currently is on the tentative list (UNESCO WHC 2018).

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Appendix Table

GenBank accession numbers of the four marker genes and associated voucher specimens/tissues that were used in this study. For more details see Guo *et al.* (2014). Sequences of species in bold are unpublished and were provided by P. Guo as personal communication.

Species names	GenBank (cytb)	GenBank (Cmos)	GenBank (NT3)	GenBank (Rag1)	Voucher
<i>Amphiesma stolatum</i>	AF471030	AF471097	-	-	CAS:HERP:206560
<i>Hebius andreae</i>	MK253674	MK253675	MK253676	MK253677	VNUF R.2017.25
<i>Hebius atemporalis</i>	KJ685680	KJ685630	KJ685732	KJ685572	GP1626
<i>Hebius atemporalis</i>	KJ685695	KJ685645	KJ685747	KJ685587	GP2318
<i>Hebius boulengeri</i>	KJ685710	KJ685660	KJ685770	KJ685609	MVZ236752
<i>Hebius boulengeri</i>	KJ685664	KJ685613	KJ685714	KJ685557	AMNH148562
<i>Hebius boulengeri</i>	-	-	-	-	AMNH192804
<i>Hebius clerki</i>	KJ685666	KJ685615	KJ685716	KJ685559	CAS215036
<i>Hebius craspedogaster</i>	KJ685704	KJ685654	KJ685759	KJ685597	GP455
<i>Hebius ‘deschauenseei’</i>	KJ685665	KJ685614	KJ685715	KJ685558	AMNH148575
<i>Hebius khasiensis</i>	KJ685669	KJ685618	KJ685719	KJ685562	CAS221525
<i>Hebius khasiensis</i>	KJ685668	KJ685617	KJ685718	KJ685561	CAS221504
<i>Hebius leucomystax</i>	-	-	-	-	AMNH R-176468
<i>Hebius metusia</i>	KJ685682	KJ685632	KJ685734	KJ685574	GP1712
<i>Hebius modestus</i>	KJ685671	KJ685620	KJ685721	KJ685564	CAS234262
<i>Hebius optatus</i>	KJ685662	KJ685611	KJ685712	KJ685555	AMNH147155
<i>Hebius venningi</i>	KJ685670	KJ685619	KJ685720	KJ685563	CAS233206
<i>Hebius ‘venningi’</i>	KJ685675	KJ685625	KJ685727	-	GP1300
<i>Herpetoreas burbrinki</i>	GQ281781	JQ687443	KJ685761	KJ685599	YBU071128
<i>Herpetoreas platyceps</i>	KJ685690	KJ685640	KJ685742	KJ685582	GP2096
<i>Natrix natrix</i>	AF471059	AF471121	EU390931	-	-
<i>Natriciteres olivacea</i>	AF471058	AF471146	-	-	CAS:HERP:220640
<i>Nerodia erythrogaster</i>	GQ285504	JN090137	-	-	-
<i>Rhabdophis tigrinus</i>	AF471051	AF471119	-	-	LSUMZ:37418
<i>Trachischium monticola</i>	JQ687435	JQ687453	-	KJ685570	GP1487
<i>Xenochrophis piscator</i>	GQ225659	GQ225669	EU390941	-	-
<i>Xenochrophis vittatus</i>	EF395895	EF395920	-	-	FMNH257460

The type specimens of the bush cricket genera *Anaulacomera* Stål, 1873 and *Furnia* Stål, 1876 (Orthoptera: Tettigoniidae) held in the Muséum d'histoire naturelle de Genève

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Abstract: All of the specimens placed in the genus *Anaulacomera* Stål, 1873 in the collection of the Muséum d'histoire naturelle de Genève had been on a long-term loan since the 1960s. The recent return of this loan allowed the identification of potential type specimens of eleven species. These are listed, the label data is given and the condition of the specimens summarised.

Keywords: Central America - Saussure - Brunner von Wattenwyl - katydids - Geneva.

INTRODUCTION

The Orthoptera collections of the Muséum d'histoire naturelle de Genève (MHNG) owe much of their richness to collecting and networking skills of Henri de Saussure (1829-1905). Having made an expedition to Mexico and the Antilles in the 1850s, Saussure remained interested in the fauna of this region, and was asked to participate in studies resulting from the collecting of the naturalists who accompanied the French military intervention in Mexico in the 1860s and in the *Biologia Centrali-Americana* series published in London by Godman and Savin towards the end of the century (Hollier & Hollier, 2013). Saussure was in contact with most of the leading entomologists of the day, and the MHNG Orthoptera collection was studied by many specialists, including his friend Carl Brunner von Wattenwyl (1823-1914), a Swiss entomologist who had lived and studied in Bern and Geneva before moving to Vienna. Saussure and Alphonse Pictet (1838-1903) even gave up their project of revising the subfamily Pseudophyllinae because Brunner von Wattenwyl had already started a similar work, and although they published their preliminary findings (Pictet & Saussure, 1892), Brunner von Wattenwyl's monograph included many specimens from the MHNG (Brunner von Wattenwyl, 1895).

In 1958 Theodore Hubbell (1897-1989) started borrowing museum specimens for a revision of the genus *Anaulacomera* Stål, 1873. This project was taken over by Harold Grant (1921-1966) and, after his untimely death, by Michael Emsley. The study intended to use specimens from the MHNG, and although no loan

forms could be found, the species name labels pinned in the insect boxes of the MHNG collection remained as witness to the borrowed specimens. The absence of potential type specimens was noted in several parts of the type catalogue of the MHNG Orthoptera (Hollier, 2011; Hollier & Maehr, 2012; Hollier & Heads, 2015). In the spring of 2018 the specimens borrowed from the MHNG were returned unexpectedly and unannounced, and it is now possible to update the information about the MHNG holdings. Of particular interest are a number of specimens of species described by Brunner von Wattenwyl, which are probably part of his type series although the deposition of specimens in Geneva was not made explicit in the original descriptions. The identification of these specimens as types is partly based on the "TYPE BRUNN:" labels, which are associated with type specimens stated to be in Geneva in the original description (Hollier & Maehr, 2012), and the fact that the MHNG, while rich in specimens from Central America, has very few specimens from Peru.

ARRANGEMENT AND FORMAT

The species are listed in alphabetic order. The format follows Hollier & Heads (2015).

The following abbreviations are used:

BMNH The Natural History Museum, London
MHNG Muséum d'histoire naturelle de Genève
NHMW Naturhistorisches Museum, Wien

CATALOGUE

angustifolia Saussure, 1859: 202 [*Phylloptera*].

Bahia. Unspecified number of ♂ and ♀.

The MHNG collection contains two specimens, both syntypes. A ♀ specimen with labels: “Bahia” [handwritten on white card]; “*Anaulacomera angustifolia* Sss.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with the wings folded; both antennae and all the legs are missing. A specimen with labels: “*Anaulacomera angustifolia* Sss.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with wings folded; most of both antennae, all the legs and the abdomen are missing. There is insect feeding damage to the thorax and the base of the wings. A detached ♂ abdomen with signs of insect feeding damage was found next to this specimen in the box in which it had been transported and, because the size suggests that it may belong to this specimen, it has been glued to a card mount on a separate pin with a handwritten label indicating its possible provenance. Box B30.

Anaulacomera angustifolia (Saussure, 1859)

angustipennis Saussure & Pictet, 1897: 341, 344-345 [*Anaulacomera*].

Guiana; Cayenne. Unspecified number of ♂.

The MHNG collection contains one ♂ syntype with labels: “CAYENNE” [printed on green paper]; “*Anaulacomera angustipennis* Sss. & Pict.” [handwritten on green card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with the wings folded; all the legs have been lost. Since the type series was unspecified, this specimen should be regarded as a syntype. Box B31.

Anaulacomera angustipennis Saussure & Pictet, 1897

brevicollis Brunner von Wattenwyl, 1878: 294 [*Anaulacomera*].

Central-Peru (Mus. Warschau). Unspecified number of ♂.

The MHNG collection contains one ♂ specimen with labels: “*Anaulacomera brevicollis* Brunn.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Possible syntype of *A. brevicollis* BvW, Hollier 2018” [handwritten on red paper]. Specimens set with the wings folded; most of both antennae, the tarsi of the left front leg, the entire right front leg and left middle leg, the tibia and tarsi of the right middle leg and the tibia and tarsi of

the right hind leg are lost. The left front wing, which lacks the tip, is detached and secured on the original pin. The species name label pinned in the box has “Pérou centr.” written on it, suggesting that the “TYPE BRUNN.” label is warranted. Box B31.

Anaulacomera brevicollis Brunner von Wattenwyl, 1878

cornucervi Brunner von Wattenwyl, 1878: 290-291 [*Anaulacomera*].

Central-Peru (Mus. Warschau). Unspecified number of ♂ and ♀.

The MHNG collection contains one ♂ specimen with labels: “cornucervi Br.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Possible syntype of *A. cornucervi* BvW, Hollier 2018” [handwritten on red paper]. Specimen (Fig. 1) set with wings folded; all three right legs are missing. The left front wing is detached and secured on the original pin. The species name label pinned in the box has “Pérou centr.” written on it, tending to support the “TYPE BRUNN.” label. Box B30.

Anaulacomera cornucervi Brunner von Wattenwyl, 1878

denticauda Saussure & Pictet, 1897: 341, 345, pl. 16, figs 15-16 [*Anaulacomera*].

Mexico, Temax in N. Yucatan (Gaumer). Probably one damaged ♂ and an unspecified number of ♀ (♂ measurements incomplete but variation in femur mentioned implying more than one ♀).

The MHNG collection contains two syntypes. A ♂ with labels: “Temax, N. Yucatan, Gaumer” [printed on white card]; “*Anaulacomera denticauda* ♂ Sss. et Pict.” [handwritten on green paper]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with left wings spread and right wings folded; the left front wing and most of the right front wing are lost. Most of both antennae, the left front leg, the claw of the left middle leg, the entire right middle leg and the left hind leg are missing. The right hind leg has been reattached with glue and lacks the claws. There is insect feeding damage to the abdomen and the cerci are broken. A ♀ with labels: “Temax, N. Yucatan, Gaumer” [printed on white card]; “*Anaulacomera denticauda* Saussure & Pictet 1897 Det. M. G. Emsley 1984” [typewritten on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “Homotype” [handwritten on white card]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with wings folded; most of both antennae and all the legs are lost. There is a ♀ syntype, erroneously referred to as the holotype on OSF, in the BMNH (images on OSF). Box B31.

Anaulacomera denticauda Saussure & Pictet, 1897



Fig. 1. Possible syntype of *Anaulacomera cornucervi* Brunner von Wattenwyl (lateral view).

erinifolia Saussure, 1859: 203 [*Phylloptera*].

Bahia. Unspecified number of ♂.

The MHNG collection contains one ♂ syntype with labels: “Bahia” [handwritten on white card]; “*Anaulacomera erinifolia* Sss.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with the wings folded; about half of the right front wing is missing. Most of both antenna, the tibia and tarsi of the left front leg, the entire right front leg, both middle legs, the entire left hind leg and the end of the tibia and the tarsi of the right hind leg are lost; the femur of the right hind leg is broken but still attached in the middle. The specimen has been repaired with glue at some time, but the repaired parts are no longer attached. The abdomen is missing. Box B30.

Anaulacomera erinifolia (Saussure, 1859)

incerta Brunner von Wattenwyl, 1878: 296, fig. 85 d-e [*Anaulacomera*].

Tenatagu (c.m. Nr. 9077), Fidji (c.m. Nr. 3926). Unspecified number of ♂ and ♀.

The MHNG collection contains two specimens. A ♂ with labels: “*Anaulacomera incerta* Brunn.” [handwritten on whitish paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Possible syntype of *A. incerta* BvW, Hollier 2018”

[handwritten on red paper]. Specimen set with the wings folded; the ends of the antennae, the tarsi of the left front leg, the last tarsal segment of the left middle leg and the last tarsal segment of the left hind leg are missing. A ♂ with labels: “*Anaulacomera incerta* Brunn.” [handwritten on whitish paper]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]. Specimen set with the wings folded; most of both antennae, the last tarsal segment of the left middle leg and two tarsal segments of the right hind leg are lost. The left hind leg, which lacks two tarsal segments, is detached and secured through the femur on the original pin. The species name label pinned in the box has “Fidji” written on it, suggesting that the “TYPE BRUNNER” label may be warranted, although it is less clear whether the second specimen, which lacks such a label, is also a potential syntype. Box B31.

Furnia incerta (Brunner von Wattenwyl, 1878)

laticauda Brunner von Wattenwyl, 1878: 292 [*Anaulacomera*].

Mexico (Mus. Genf, Wien), Orizaba (c.m. Nr. 7151), St Jean (Columbia, Mus. Berlin). Unspecified number of ♂ and ♀.

The MHNG collection contains three specimens that can be identified as syntypes. A ♂ with labels: “Mexique, Sumichrast” [handwritten on white paper]; “*laticauda* Br.” [handwritten on green paper]; “*Anaulacomera laticauda* Br. 1878 Det. M. G. Emsley 1984” [typewritten

on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with the wings folded; most of both antennae, both front legs, the right middle leg, the tibia and tarsi of the left hind leg and the tarsi of the right hind leg are missing. There is insect feeding damage to the thorax. A ♂ with labels: “Bilimek Mexico 1871, Cuernavacca” [printed on white card with “Cuernavacca” handwritten]; “Anaulac. laticauda Br.” [handwritten on white card with printed margins]; “Anaulacomera laticauda Br. 1878 Det. M. G. Emsley 1984” [typewritten on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “# 8” [handwritten on white paper]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with left front wing spread and the others folded; both antennae, the tibia and tarsi of the left middle leg, the entire right middle leg and both hind legs are missing. A ♀ with labels: “Anaulacomera laticauda Brunn.” [handwritten on green paper]; “TYPE BRUNN:” [printed on white card]; “Anaulacomera laticauda Br. 1878 Det. M. G. Emsley 1984” [typewritten on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Syntypus” [printed on red paper]. Specimen set with the wings folded; most of both antennae, the last tarsal segment of the left front leg, the tibia and tarsi of the right front leg and all of both hind legs are missing. There is insect feeding damage to the abdomen. The other eight specimens under this name have data labels characteristic of the specimens collected for the *Biologia Centrali-Americana* or stating that the specimens were collected by Fruhstorfer, and were therefore collected after the publication of the original description.

Anaulacomera laticauda Brunner von Wattenwyl, 1878

lativertex Brunner von Wattenwyl, 1878: 292-293 [*Anaulacomera*].

Santa Fe de Bogota (c.m. Nr. 4805). Unspecified number of ♂.

The MHNG collection contains one ♂ specimen with labels: “COLOMBIE, 603.28” [printed on white card with numerals handwritten]; “lativertex Br.” [handwritten on green paper]; “Type Brunner” [handwritten on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “Possible syntype of *A. lativertex* BvW, Hollier 2018” [handwritten on red paper]. Specimen set with the wings folded; the ends of both antennae are lost. The MHNG acquisition register number 603.28 records a purchase of 86 pinned Orthoptera collected in Colombia with the date 1879. That would appear to make it impossible for this specimen to be a syntype, but there is much evidence that the registers were often written up in arrears and the specimens may have arrived sooner.

Anaulacomera lativertex Brunner von Wattenwyl, 1878

securifera Brunner von Wattenwyl, 1878: 289 [*Anaulacomera*].

Central-Peru (Mus Warschau). Unspecified number of ♂. The MHNG collection contains two ♂ specimens, both possible syntypes. A ♂ with labels: “securifera Br.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Possible syntype of *A. securifera* BvW, Hollier 2018” [handwritten on red paper]. Specimen set with wings folded; the ends of both antennae, the entire left front leg, the tarsi of the right front leg, the entire left middle leg, the tibia and tarsi of the right middle leg and all of both hind legs are missing. The left front wing is detached and glued to a card mound on the original pin. A ♂ with labels: “Anaulacomera securifera Br.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Possible syntype of *A. securifera* BvW, Hollier 2018” [handwritten on red paper]. Specimen set with the wings folded; both antennae, both front legs, the tibia and tarsi of the left middle leg, the entire right middle leg and both hind legs are missing. There is insect feeding damage to the abdomen, which has been repaired with glue. The species name label pinned in the box has the locality “Pérou” handwritten on it, tending to support the “TYPE BRUNN” labels. Box B30.

Anaulacomera securifera Brunner von Wattenwyl, 1878

sulcata Brunner von Wattenwyl, 1878: 289-290 [*Anaulacomera*].

Brasilien (Mus. Wien, c.m. Nr. 1097), Peru (Mus. Warschau). Unspecified number of ♂ and ♀.

The MHNG collection contains two specimens. A ♂ with labels: “sulcata Br.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Possible syntype of *A. sulcata* BvW, Hollier 2018” [handwritten on red paper]. Specimen set with left front wing spread and other wings folded; most of both antennae, both front legs and both hind legs are missing. The left middle leg is detached and glued to the “TYPE BRUNN:” label. There is insect feeding damage to the thorax and abdomen. A specimen with labels: “Anaulacomera sulcata Br.” [handwritten on green paper]; “TYPE BRUNN.” [printed on white card]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]; “Possible syntype of *A. sulcata* BvW, Hollier 2018” [handwritten on red paper]. Specimens set with wings folded; most of both antennae, the left front leg, both middle legs and the tarsi of both hind legs are missing. The end of the abdomen is lost and there is insect feeding damage to what remains. The left front wing is detached and secured on the original pin. The species name label pinned in the box has “Amer. mérid.” written on it,

suggesting that the “TYPE BRUNN:” label is warranted. Box B30.

Anaulacomera sulcata Brunner von Wattenwyl, 1878

There are other specimens of interest amongst those returned.

A ♀ in box B30 has labels: “Pernambuco” [handwritten on white card]; “*Anaulacomera inversa* ? Brunn.”; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]. This specimen was described by Brunner von Wattenwyl (1878: 285) immediately after his description of *A. inversa* based on ♂ specimen(s) from Brazil deposited in the NHMW. Brunner von Wattenwyl stated that the ♀ specimen in MHNG was very similar to the ♂, but he was not sure if it was the same species and the specimen is therefore not a syntype.

A ♂ in box B31, has labels: “Bugaba, 800-1500 ft., Champion” [printed on white card]; “*Anaulacomera laticauda* var *nodosa* Sss.” [handwritten on green paper]; “PROPERTY MUS. HIST. NAT. GENF” [printed on white card]; “MICH” [typewritten on yellow paper]. Although this specimen is one that was described as a variety in Saussure & Pictet (1897: 344), it was not named in that publication, which means that it is not a type specimen and the name is not available.

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An ancient radiation: Ortholasmatine harvestmen in Asia - a new genus, three new species and a revision of the known species (Arachnida, Opiliones, Nemastomatidae)

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Abstract: The Asian Ortholasmatinae fall into two groups which are attributed to different genera: *Cladolasma* Suzuki, 1963 from Japan and *Asiolasma* gen. nov. The latter is established as a new genus to encompass six mainland Asian species, with a relatively homogeneous male genital morphology, that are different from *Cladolasma* and from all New World ortholasmatines. Seven Asian species are characterized, four of them redescribed: *Cladolasma parvulum* Suzuki, 1963 (Shikoku Is., southern Japan), *Asiolasma angka* (Schwendinger & Gruber, 1992) comb. nov. (northern Thailand), *A. damingshan* (Zhang & Zhang, 2013) comb. nov. (Guangxi, southern China), *A. ailaoshan* (Zhang, Zhao & Zhang, 2018) comb. nov. (southern Yunnan, China). Three species are described as new: *A. juergengruberi* (northern Yunnan, China; male and female), *A. schwendingeri* (northern Vietnam; male and female) and *A. billsheari* (southern Gansu, China; male). All species are illustrated and keyed. Apparently the Ortholasmatinae is a relict group in Asia, represented by morphologically similar and geographically scattered species. A phylogenetic old age is indicated by plesiomorphic character states (poorly developed keel cell network; simple male genitalia with uniform armature; hood at anterior margin of prosoma with lateral apophyses, interconnected by tubercles at the basis of the apophyses which form minute bridges; species restricted to moist forest litter on mountains). It is assumed that ortholasmatines have originated in what is presently Southeast and East Asia where they now represent a relict group; presumably they arrived in the New World later. American species show a number of apomorphic characters which are largely lacking in Asian species. Species in Asia survive in forest formations from tropical (southern China, northern Vietnam, northern Thailand) to subtropical (southern Japan) and to temperate climate conditions (southwestern and northwestern China). Primeval montane forests with a closed canopy and a moist litter layer are important habitat requirements. Except for two species, only single locality records are known.

Keywords: Taxonomy - genital morphology - historical biogeography - relicts - soil fauna - Japan - Thailand - Vietnam - China - New World.

INTRODUCTION

The Ortholasmatinae, family Nemastomatidae, are mostly distributed in the temperate parts of the New World where this group was first discovered. This paper aims at a better characterization of Asian species, of which only few were hitherto described. In addition, it presents not only three new species from northern Vietnam and various parts of central and southern China, but also a new genus to accommodate most of the Asian species. The relationships and historical geography of Asian and American representatives of the subfamily, mainly of the genus *Dendrolasma* Banks, 1894b, is likewise addressed.

TAXONOMIC HISTORY

The bizarre-looking soil-bound ortholasmatine harvestmen are peculiar members of the opilionid faunas of western North and Central America, where a large number of species were documented and well-studied (Shear & Gruber, 1983; Shear, 2010; Cruz-López, 2017). From there the first species were described in 1894 by Banks (1894a, b). He established the genera *Ortholasma* Banks, 1894a and *Dendrolasma* Banks, 1894b, each based on a new species. These were followed by further New World discoveries, altogether 20 valid species currently known from the Americas (Shear & Gruber 1983, 1987; Shear 2006, 2010; Cruz-López, 2017; Cruz-López *et al.*, 2018). The presence of Ortholasmatinae in Asia, however,

remained unknown for a long time and was first documented in 1963 from the island of Shikoku, southern Japan by Suzuki, who named *Cladolasma parvula* (correct: *parvulum*) Suzuki, 1963, and later (Suzuki 1974) placed it in the genus *Dendrolasma*. Nearly 30 years later, Schwendinger & Gruber (1992) presented the first species from mainland Asia: *Dendrolasma angka* Schwendinger & Gruber, 1992 from northern Thailand. While *Ortholasma* and *Dendrolasma* were regarded as New World taxa, the authors mentioned differences between *D. angka* and American *Dendrolasma*, mainly in the structure of the pedipalps and of the dorsal exoskeleton, namely, the free, isolated metapeltidium, and in a specialized male genital conformation. Consequently, Schwendinger & Gruber (1992) placed their new Thai species in *Dendrolasma*, not in the Japanese *Cladolasma*, which then was still in the synonymy of *Dendrolasma*, and followed Suzuki (1974). However they recognized no close relationship between the Thai species and the American *Dendrolasma*. Males of *D. angka* were not available at that time to allow a detailed phylogenetic analysis and an alternative taxonomic placement. Subsequently, Shear (2010) excluded the Thai *D. angka* from *Dendrolasma*, revalidated *Cladolasma* and added *D. angka* to this genus, thus restricting its distribution to Asia. More recently, two additional species were described from China, *C. damingshan* Zhang & Zhang, 2013 from Guangxi Province and *C. ailaoshan* Zhang, Zhao & Zhang, 2018 from Yunnan Province, both correctly assigned to *Cladolasma*, albeit without discussing the characters that would make them congeneric with the quite peculiar *C. parvulum* from Japan.

In the present paper, I characterize (by also including male genital characters) seven species from mainland Asia (Thailand, Vietnam, China) and point out the distinctive features of the sole Japanese ortholasmatine. Obviously, they all belong to two different morphological entities, *C. parvulum* on the one side opposed to all mainland Asian populations on the other side. Strong differences are evident in male genital morphology, which is uniform in the mainland species and markedly different from that of *C. parvulum*. For the mainland Asian species I propose a new genus, the species of which are quite uniform by their external morphology and in details of penis morphology. The mainland Asian species are largely scattered and cover a large area ranging from northern Vietnam and northern Thailand to central China in the Qinling Mountains. The climate in these areas is tropical and subtropical in the southern part and temperate in the northern part. I support the original hypothesis of Shear & Gruber (1983) that ortholasmatine harvestmen might have evolved in what is presently tropical and/or subtropical East Asia, spread to the New World where they underwent a remarkable morphological and ecological radiation, as well as a range expansion. There they occur between near the Alaskan border in the North to México and Honduras in the South, with the greatest diversity

currently known from Central America, represented by several species in four genera (Shear & Gruber, 1983; Shear, 2010; Cruz-López *et al.*, 2018; see Discussion).

MATERIAL AND METHODS

Original line drawings were done with the help of a camera lucida attached to a Carl Zeiss research microscope, whereas the automontage photographs were taken with a Leica Z6 APO A in Admannshagen (J. Schmidt) and in Geneva (P. Schwendinger). Measurements were taken by means of a micrometer disc attached to a Leitz stereo microscope, those of the penis from the original drawings. In addition to the material collected by myself, specimens treated here were handed over to me for study by Peter Schwendinger (Geneva; MNHG), David W. Wrase (Berlin) and Chao Zhang (Baoding; MHBUS). All measurements are given in mm.

Abbreviations of morphological terms

Cx	coxa
do	dorsal
Fe	femur
la	lateral
Mt	metatarsus
Op gen	operculum genitale
Pt	patella
Ta	tarsus
Ti	tibia
Tu oc	tuber oculorum, ocularium
Tr	trochanter
ve	ventral

I, II ... XII denominate January, February ... December

Museum acronyms

CJM	Working collection of J. Martens, Mainz, Germany
MHBUS	Museum of Hebei University, Baoding, China
MNHG	Muséum d'histoire naturelle de Genève, Switzerland
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

TAXONOMIC PART

Family Nemastomatidae Simon, 1872

Subfamily Ortholasmatinae Shear & Gruber, 1983

Genus *Cladolasma* Suzuki, 1963

Cladolasma Suzuki, 1963: 40. – Suzuki, 1974: 121 (synonymisation with *Dendrolasma* Banks, 1894b). – Shear, 2010: 16 (revalidation of *Cladolasma*).

Type species: *Cladolasma parvulum* Suzuki, 1963 (by original designation and monotypy).

Remarks: A genus of Nemastomatidae, subfamily Ortholasmatinae, according to the present revision

Key to the currently known Asian Ortholasmatinae species (based on male characters)

- 1A Strongly asymmetric glans penis (in do and la views) with eight strong spines arranged in two narrow rows and a distal chaplet of four slightly smaller spines, stylus not twisted (Figs 6-8), tubercles at posterior opisthosomal margin club-shaped (Figs 2, 5); distributed in southern Japan, Shikoku..... *Cladolasma parvulum*
- 1B Symmetric glans penis with weaker spines arranged in several separated rings (do, ve and la views, Figs 20-22, 38-40, 47-49, 78-83, 94-96, 106-108), tubercles at posterior opisthosomal margin digitiform, tapering towards tip (Figs 17, 19, 26, 31-34, 53-54, 60-61, 63, 65, 88-89, 91-92, 104-105); distributed in mainland Asia 2
- 2A Dorsal apophysis on top of 2nd cheliceral article massive and markedly elevated, ending in a strong pointed hook (Figs 55-56, 72-75, 77, 112-114)..... 3
- 2B Dorsal apophysis of 2nd cheliceral article represented only by a small pointed, not elevated hook (Figs 27, 35, 100)..... 5
- 3A Hook on dorsal apophysis of 2nd cheliceral article directed forward, immediately below the hook an additional blunt low apophysis (Figs 112, 114), a small pointed apophysis prolaterally-distally on pedipalpal patella (Figs 115, 117); known from southern Gansu, China..... *Asiolasma billsheari* sp. nov.
- 3B Hook on dorsal apophysis of 2nd cheliceral article directed more or less downward (Figs 55-56, 72-74), no apophysis on pedipalpal patella (Fig. 58)..... 4
- 4A Hook on a rounded and slightly angular cheliceral apophysis directed downward, more or less parallel to front of 2nd cheliceral article (Figs 55-56), a low apophysis with a short seta on dorsal side of basal cheliceral article (Figs 55-56); known from southern Yunnan *Asiolasma ailaoshan*
- 4B Hook of rounded apophysis inclined, forming an obtuse angle against front of 2nd cheliceral article (Figs 72-74, 77), a markedly elevated apophysis carrying a relatively long seta on dorsal side of basal cheliceral article (Figs 72-75); known from northern Yunnan, China..... *Asiolasma juergengruberi* sp. nov.
- 5A Body markedly globular (Fig. 26), dorsal side of scutum with several groups of pointed tubercles (Fig. 26), known from a single mountain in northern Thailand *Asiolasma angka*
- 5B Body of male not globular, flat (Fig. 92), dorsal side of scutum without several groups of pointed tubercles (Fig. 34) 6
- 6A Pedipalp stout, its tibia and tarsus slightly inflated, relatively short (Fig. 37), body small, about 3.1 mm (Fig. 31); known from southern Guangxi, China *Asiolasma damingshan*
- 6B Pedipalp of male slender, tibia and tarsus not inflated, relatively long (Fig. 102), body relatively large, about 3.4-3.6 mm (Fig. 32); known from northern Vietnam *Asiolasma schwendingeri* sp. nov.

comprising one Asian species. The gender of the generic name is neuter.

Extended diagnosis: A genus of Ortholasmatinae with metapeltidium free, neither joined to prosoma nor to opisthosoma; medium-sized species (up to 3.5 mm body length, females larger than males); hood on prosoma short, its lateral apophyses interconnected by bridges at their bases; prosoma with one long apophysis on each side of hood at anterior border; tibia and tarsus of pedipalps with dense cover of clavate setae, not sexually dimorphic, both sexes with ve gland in palpal patella; lattice pattern of interconnected keel cells inconspicuous, the individual anvil-shaped tubercles low, often dorsally rounded and unspecialized. Apophyses at posterior margin of opisthosoma short, slightly inflated at the end, club-shaped.

Genital morphology of males: Characterized by rather

unspecialized penis, rather slender, parallel-sided; muscle-containing base of penis relatively long, only slightly inflated, deeply incised, occupying about one fourth of truncus length; truncus in straight continuation of inflated base (in do/ve view). Armature of glans markedly asymmetrical, with strong spicules concentrated on do sides, slightly shorter ones near base of stylus.

Included species: *Cladolasma parvulum* Suzuki, 1963.

Relationships: With regard to genital morphology, *C. parvulum* is separated from all mainland Asian ortholasmatine species. A dorsoventrally asymmetric glans and marked difference in size and arrangement of glans spicules makes this penis different from those of all other Asian and American species. I judge the differences to be strong enough to allot generic ranks to the sole Japanese species and to the presently known six mainland Asian species.

***Cladolasma parvulum* Suzuki, 1963**

Figs 1-15

Cladolasma parvula Suzuki, 1963: 41 (description of juveniles; types not examined). – Shear, 2010: 17 (revalidation of genus, discussion of phylogenetic placement). – Zhang & Zhang, 2013: 450 (comparison with a Chinese species). – Schönhof, 2013: 24 (species listing).

Dendrolasma parvula (Suzuki, 1963). – Suzuki, 1974: 121 (transfer and redescription of species based on adults; synonymisation of *Cladolasma* with *Dendrolasma*).

Dendrolasma parvulum (Suzuki, 1963). – Shear & Gruber, 1983: 60 (figures, discussion of phylogenetic placement).

Material examined: CJM 2759; 1 male, 1 female; JAPAN, Shikoku, Ehime Pref., Mt Saragamine, beech forest, 1160 m; 33°49' N, 132°46' E; N. Tsurusaki; leg. 7.10.1983.

Remark: The species was correctly described by Suzuki (1963, 1974) and by Shear & Gruber (1983) in many details, but for a comparison with the mainland Asian species an extended description and additional drawings and images created by photo stacking are added here.

Diagnosis: Characterized by male genital morphology (spicules of penis in two groups of similar sizes and arrangement and an additional distal chaplet of four spicules) and by tubercles on dorsal side of scutum

(arranged irregularly, no distinct lattice of keel cells, scanty anvil-shaped tubercles).

Description**MALE**

Body, dorsal side (Figs 2, 4-5): Compared to *Asiolasma* species rather flat, corona analis and sternites markedly extended and causing a slightly inflated and elevated opisthosoma (la view); Tu oc slightly elevated; hood extending from anterior margin of prosoma and including a rather short hood after a short ascent running parallel to prosoma, carrying one distal and five lateral apophyses, the distal one longest, the lateral ones consecutively shorter in direction to basis, interconnected by small anvil-shaped bridges close to the basis of individual apophyses; a pair of long and massive, slightly fusiform apophyses extending from anterior margin of prosoma to about two-thirds of hood length. Posterior margin of opisthosoma with a row of about 15-17 massive tubercles of various lengths, slightly inflated at the apex, longest ones in mid-part of row; all apophyses of hood and rear end of opisthosoma covered with a dense coat of pointed, posteriad-directed denticles.

Lattice cell network of anvil-shaped tubercles inconspicuous (Figs 2, 4-5), formed by low rounded tubercles and only rarely by interconnected anvil-shaped tubercles, most cells not clearly defined, if present irregularly shaped, tubercles forming only dense or loose



Fig. 1. Distributional records of ortholasmatine species in East and Southeast Asia. (1) *Asiolasma billsheari* sp. nov., China, Gansu, Qinling range. (2) *A. juergengruberi* sp. nov., China, Yunnan, above Lugu Hu. (3) Same species as before, China, north of Lijiang. (4) *A. ailaoshan*, China, Yunnan, Ailao Shan. (5) *A. damingshan*, China, Guangxi, Daming Shan. (6) *A. schwendingeri* sp. nov., Vietnam, Mt Ba Vi. (7) *A. angka*, Thailand, Doi Inthanon. (8) *Dendrolasma parvulum*, Japan, Shikoku Island.

agglomerations; on metapeltidium only a transverse row of tubercles, no cells; tubercles slightly darker than surface of prosoma and opisthosoma.

Body, ventral side: Cx front and back side with a row of tubercles, longest on Cx I in front, in addition with dense cover of low rounded tubercles, Op gen with low tubercles, free tergites bent to ventral side, with rear row of low tubercles, most pronounced on corona analis.

Mostly long rounded tubercles on Cx: I 1 pro-la, 1 retro-la, II 1 retro-la especially large, III -, IV 1 pro-la. Tubercles on Tr: I retro-la, II -, III 1 pro-la and retro-la each, IV 1 pro-la.

Chelicera (Fig. 12): Basal article in posterior part dorsally slightly enlarged (la view), do side markedly constricted, saddle-shaped (la view), four strong pointed tubercles on distal part dorso-prolaterally, with few setae laterally and prolaterally, no brush of setae, no obvious glandular tissue. Second article with a strong stumpy apophysis on upper front pointing to ve side. Setae of various sizes, mainly on frontal surface.

Pedipalp (Fig. 14): Tr slender, slightly swollen on do side; three pointed small tubercles on ve side, each with as strong seta; Fe strong and massive, relatively short, continuously widening toward apex, slightly bent downwards, loosely set with few scattered normal hairs except for a group of strong setae mediodistally; Pt slightly enlarged and strongly bulge-like ventrally in central part, glandular tissue recognizable below cuticle in enlarged ve part (outlined in Fig. 14); Ti cylindrical but slender, with indistinct basal stalk, not curved, dense cover of clavate setae concentrated in distal part; Ta slightly more slender than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round (mostly omitted in Fig. 14).

Legs: Rather short, all articles cylindrical; Fe widened distally, particular on legs I, III and IV; Tr of all legs set with rounded tubercles of various sizes, largest ones distally, all densely covered with massive microtrichia (Figs 4-5); Fe, Pt and Ti of all legs densely covered with fine microtubercles similar to those on Tr, tubercles with fine microsetae interspersed; Mt and Ta only with fine setae.

Genital morphology (Figs 6-11): Penis long and slender, strait, slightly depressed, markedly parallel-sided all over its length (do/ve and la view); basis slightly broadened, deeply split into two parts, containing nearly the entire portion of the two muscles, from there truncus slightly tapering towards glans (do/ve view) and glans towards stylus; glans spindle-shaped and broadened only in la view; stylus short, no helical torsion. Apex of penis with long spindle-like spicules of slightly different sizes and arranged into two groups: i) distally six spicules symmetrically arranged in a chaplet on la, do and ve side, ii) proximally two parallel rows of four larger spicules each, two of them on la side, others on ve side.

FEMALE (Figs 3, 13, 15)

Similar to male; club-shaped tubercles on posterior

margin of opisthosoma shorter than in male (Fig. 3); chelicera (Fig. 13) similar to those of male, including tubercles on basal article, no hook on 2nd article; pedipalp (Fig. 15) as in male, but Fe less bent, less enlarged distally, Pt also enlarged ventrally but less so than in male, glandular tissue also recognizable below cuticle, few clavate setae ventrally. Opisthosoma more arched, giving the impression of a more globular body.

Measurements: Body length of male 3.0 (n=1), female 3.5 (n=1). Leg II length of male, female in parentheses: Fe 2.4 (2.2) Pt 0.7 (0.7) Ti 2.2 (-) Mt 1.5 (-) Ta 1.0 (-). Penis length 1.7.

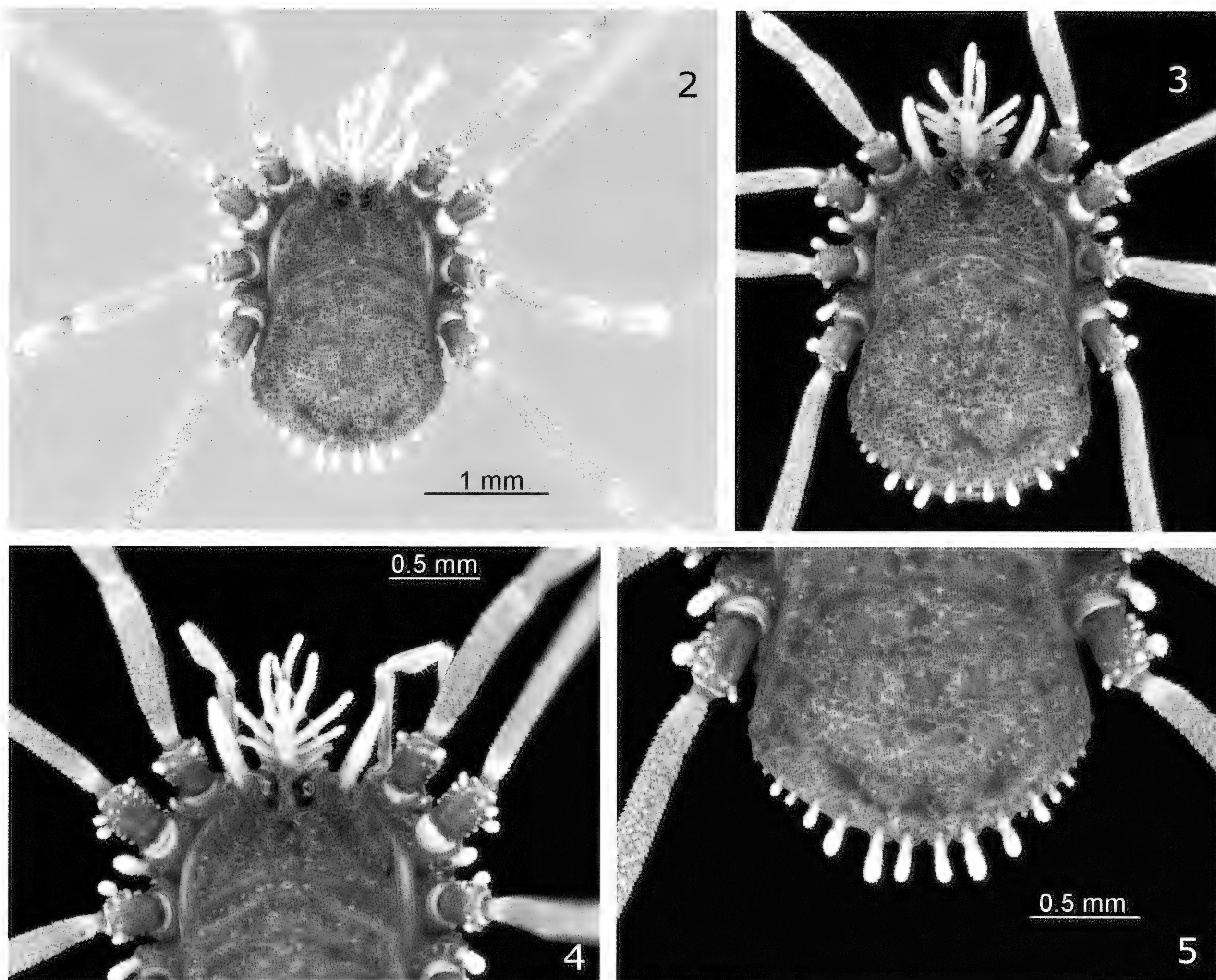
Variation: Little variation was observed in male genital morphology. All drawings presented by Suzuki (1974), Shear & Gruber (1983) and in this paper, especially concerning spicules on the glans (Figs 6-11), are very similar even in minor details. This may be due to the restricted genepool caused by minute distributional areas of this species. Branches of the hood in some specimens are asymmetrical and uneven on the left and the right side (Figs 2-4), single branches are bent toward the mid-axis. The specimens examined have only few clavate setae on their pedipalpal articles but specimens illustrated in Shear & Gruber (1983: figs 202-203) have many on Fe, Pt and Ti. The latter may be due to abrasion in alcohol-preserved specimens.

Distribution (Fig. 1): This species is confined to Shikoku Island, southern Japan, where the distributional ranges of its populations seem to be rather small. Mt Ishizuchi is mentioned in the original description; N. Tsurusaki provided a series of specimens from Mt Saragamine for study (see photographs and drawings). According to information presented by Suzuki (1963, 1974), the species is confined to moist and cool montane forests, mainly beech (*Fagus crenata*), with a rich understorey of various grass species, roughly between 1200 m and 1500 m altitude.

Genus *Asiolasma* gen. nov.

Type species: *Dendrolasma angka* Schwendinger & Gruber, 1992.

Diagnosis: Asian Ortholasmatinae with free metapeltidium not joined to prosoma or to opisthosoma. Characterized by an unspecialized penis with a rather short, slightly twisted stylus, opening of seminal duct sub-terminal; spicules on apex of penis rather long on do, ve and la sides of glans (rarely on distal part of truncus), in most cases symmetrically arranged in three (rarely four) groups on glans and on distal part of truncus, rather uniform in all known species; network of anvil-shaped denticles on do side of body present, cells not strongly symmetrical, appearing somewhat disorderly, individual cell-forming denticles low in most



Figs 2-5. *Cladolasma parvulum*. (2) Body of male in dorsal view. (3) Body of female in dorsal view. (4) Prosoma of male in dorsal view. (5) Opisthosoma of male in dorsal view. Photographs by J. Schmidt.

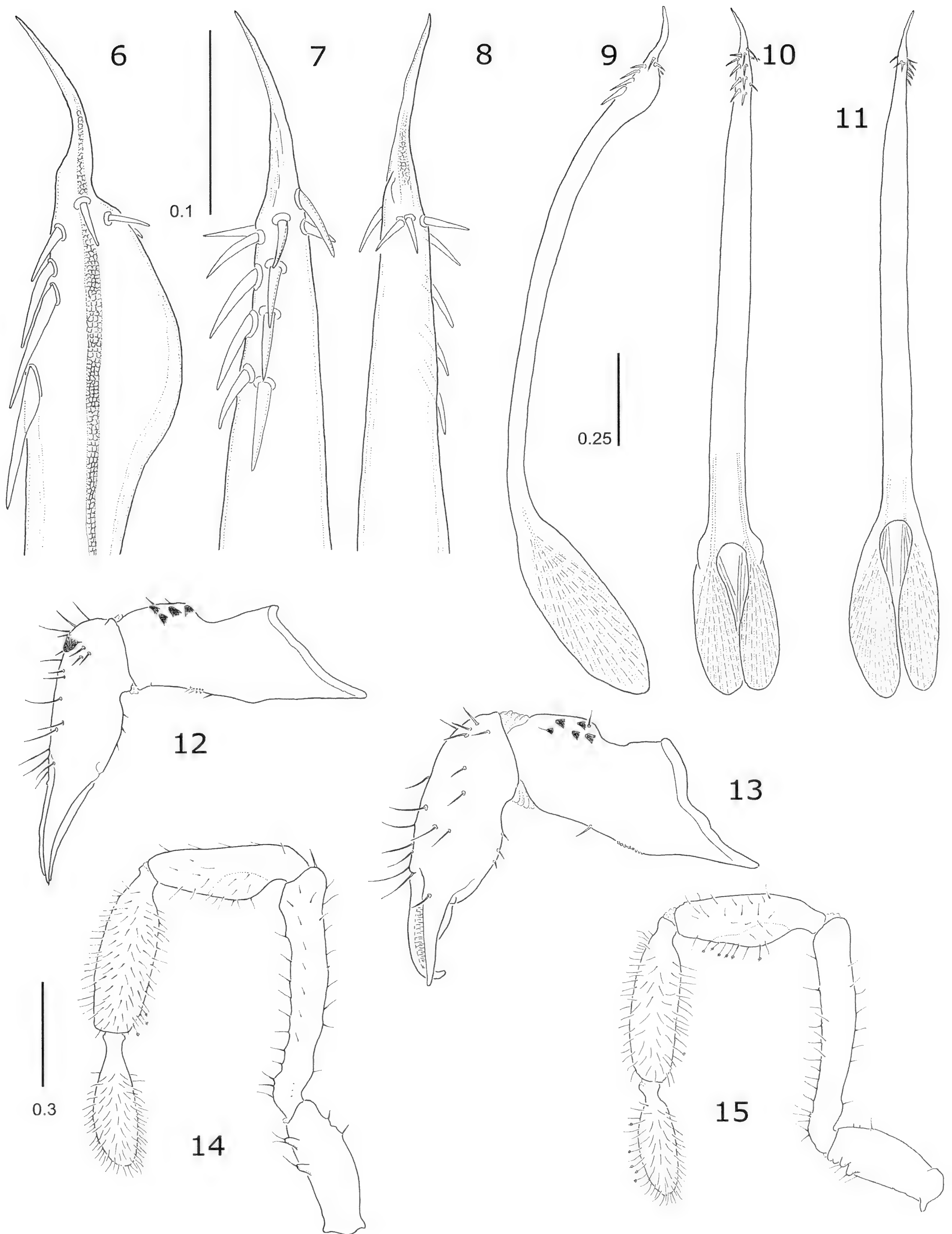
species, thus without marked sculpture on opisthosomal scutum.

Name: It is derived from Asia, the continent where the species of this genus live, and the Greek noun “elasma”, a plate, mainly of metal, referring to the hood on the anterior margin of the prosoma. The name is in analogy of the other generic names of Ortholasmatinae. The gender of the name is neuter.

Distribution (Fig. 1): The six hitherto known species occur in northern Thailand (Doi Inthanon), northern Vietnam, as well as southwestern and southern China (Yunnan, Guangxi and Gansu provinces, respectively). The few available records are highly scattered and span a geographically and climatically large and diverse area from the tropics/subtropics in Vietnam, southern China and northern Thailand to high altitudes of temperate mountain ranges in central southwestern and partly

southern China. According to current knowledge, *Asiolasma* species are confined to mountainous areas between 1200 m and 3300 m in China, 900 m in northern Vietnam, 2400-2500 m in northern Thailand, and the sole *Cladolasma* species has been recorded at 1200-1500 m on Shikoku Island, Japan.

Relationships: Judging from male genital morphology and formation of the hood, all *Asiolasma* gen. nov. species known at present seem to be closely related with each other. These characters seem to be rather uniform, although differences between species are present. Specific distinctions are also found in body shape, body size, equipment of body with a lattice work of anvil-shaped tubercles, size and shape of pedipalps and pattern of setae on pedipalpal articles, presence or absence of pedipalpal glands and shape of apophyses on chelicerae. These need to be carefully identified.



Figs 6-15. *Cladolasma parvulum*, male (6-12, 14), female (13, 15). (6) Glans penis in lateral view. (7) Same in dorsal view. (8) Same in ventral view. (9) Truncus penis in lateral view. (10) Same in dorsal view. (11) Same in ventral view. (12) Right chelicera of male in prolateral view. (13) Same of female. (14) Right pedipalp of male in prolateral view. (15) Same of female. Scales: 0.25 mm (9-11); 0.1 mm (6-8); 0.3 mm (12-15).

The *Asiolasma* gen. nov. species can be divided into two groups. Three of the southern species display only a pointed hook on the upper side of the 2nd cheliceral article (*A. angka* [Fig. 27], *A. damingshan* [Fig. 35], *A. schwendingeri* sp. nov. [Fig. 100]; in the single northern species (*A. billsheari* sp. nov. [Fig. 112] and in two of the southern species this hook is present as well but situated on a massive rounded apophysis (*A. juergengruberi* sp. nov. [Figs 72-74], *A. ailaoshan* [Figs 55-56]). The Japanese *Cladolasma parvulum* stands apart and differs markedly in genital morphology, in a little developed do network of anvil-shaped tubercles and in a small anterior hood (see above).

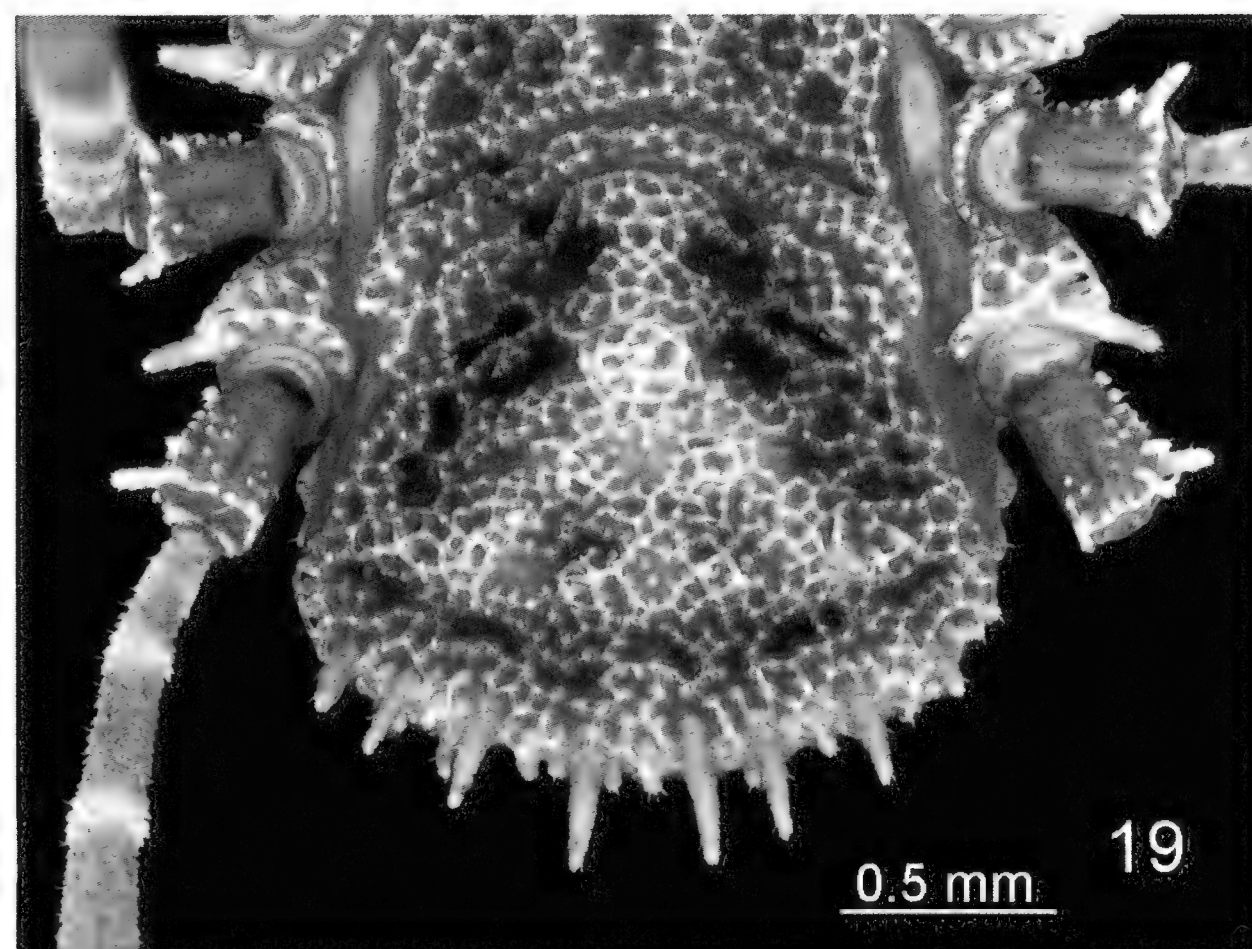
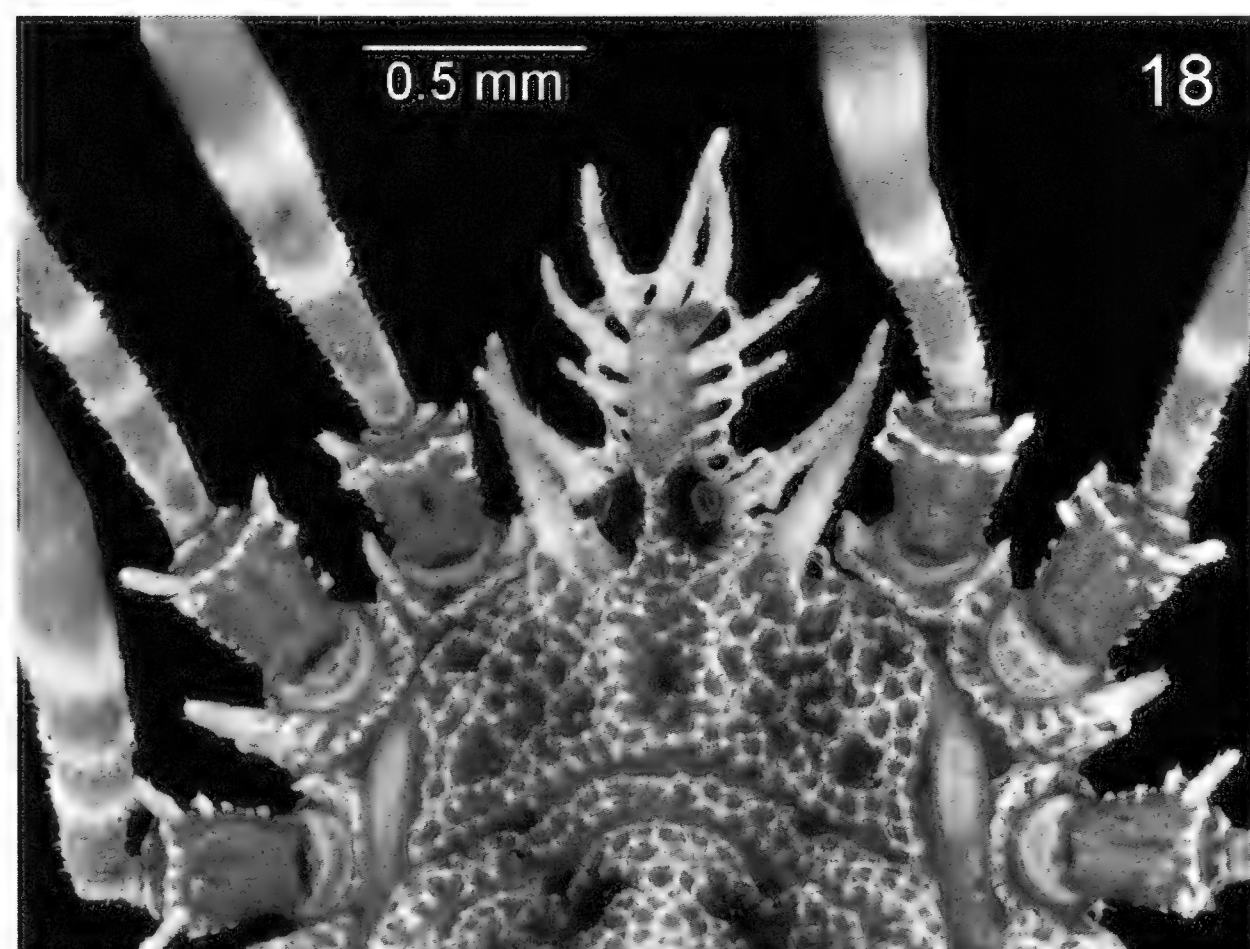
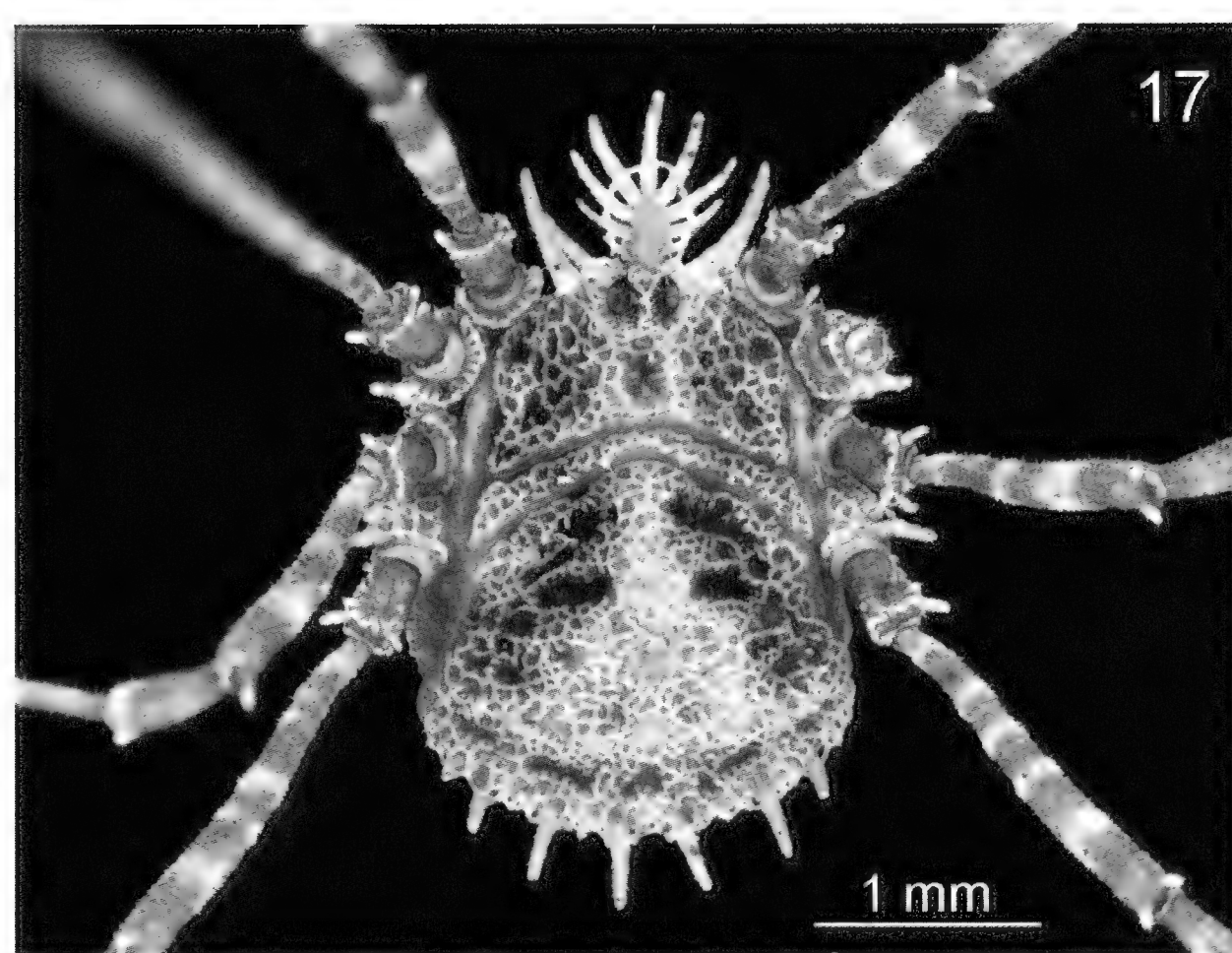
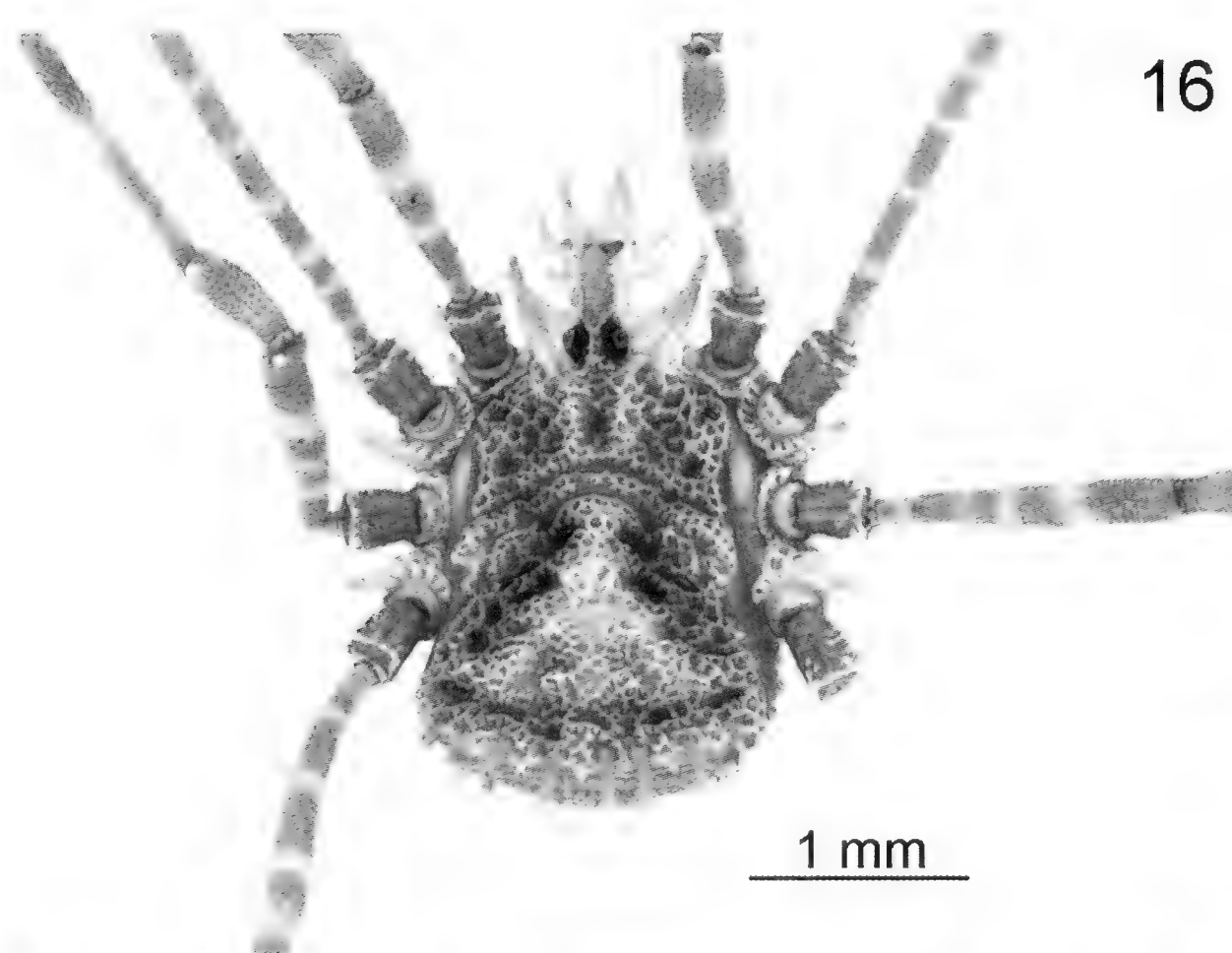
All species of the American ortholasmatine genera *Ortholasma* Banks, 1894a, *Dendrolasma* Banks, 1894b, *Trilasma* Goodnight & Goodnight, 1942, *Martensolasma* Shear, 2006 and *Cryptolasma* Cruz-López, Cruz-Bonilla & Francke, 2018 clearly differ from Asian species by the following characters: i) the penis is much more slender, the inflated base shorter, the stylus formed like a barbed hook (not so in *Dendrolasma*), the armature of the glans

is more diversified and the spicules often of different size and pattern (uniform in *Ortholasma*); ii) many (up to twelve on each side) apophyses are present on the hood, the single distal and all following lateral apophyses of the hood are interconnected by fine bridges only at the distal end of the apophyses (hood lacking in *Martensolasma*); iii) the network of closed keel cells formed by anvil-shaped tubercles on the do scutum is regular, distinctly symmetrical and ornamental, the individual tubercles markedly elevated, resulting in a distinct and elaborate structure of the network (for all characters compare multiple details in Shear & Gruber, 1983 and Shear, 2010).

***Asiolasma angka* (Schwendinger & Gruber, 1992)
comb. nov.**

Figs 1, 16-30

Dendrolasma angka Schwendinger & Gruber, 1992: 57 (description of female).

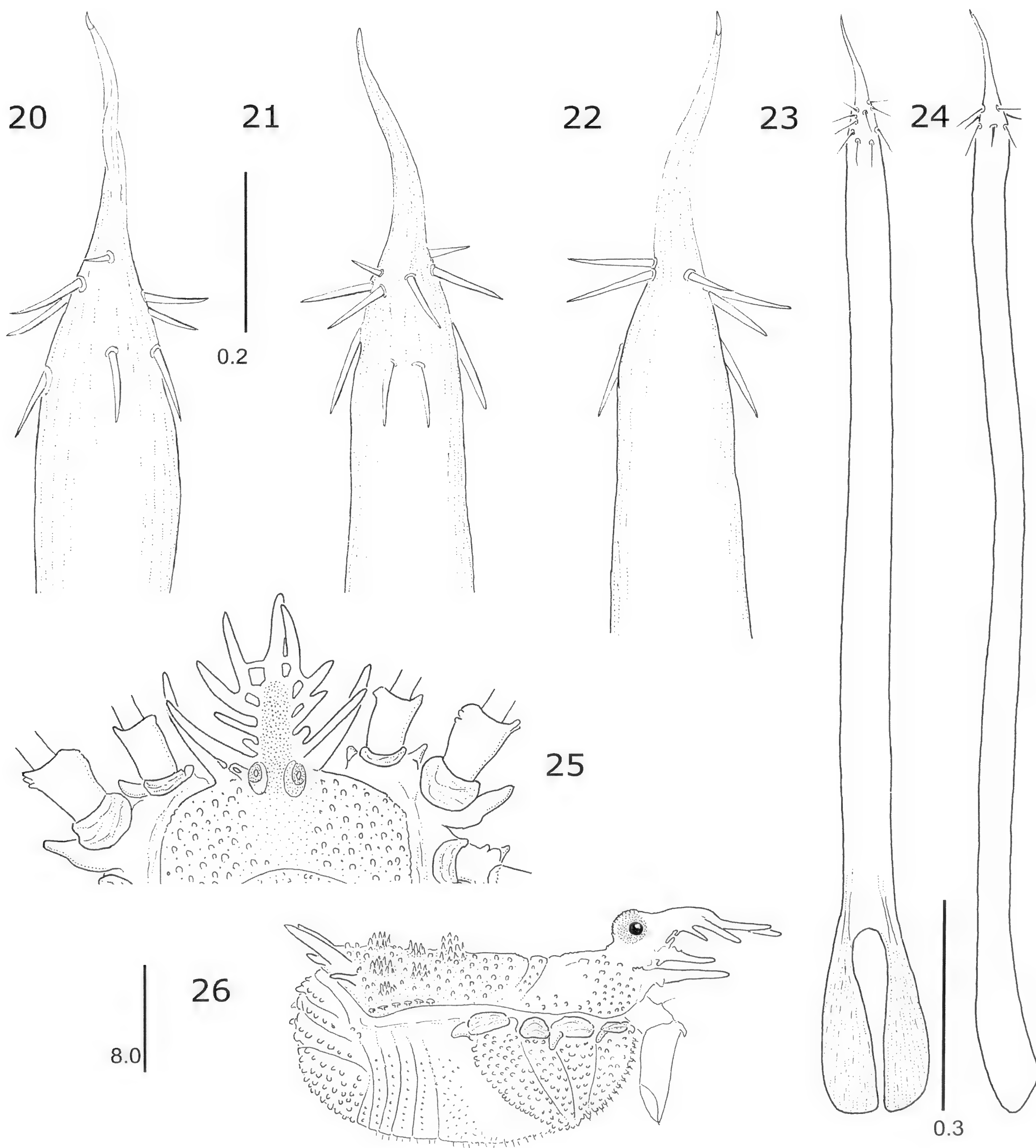


Figs 16-19. *Asiolasma angka*. (16) Body of male in dorsal view. (17) Body of female in dorsal view. (18) Prosoma of male in dorsal view. (19) Opisthosoma of male in dorsal view. Photographs by J. Schmidt.

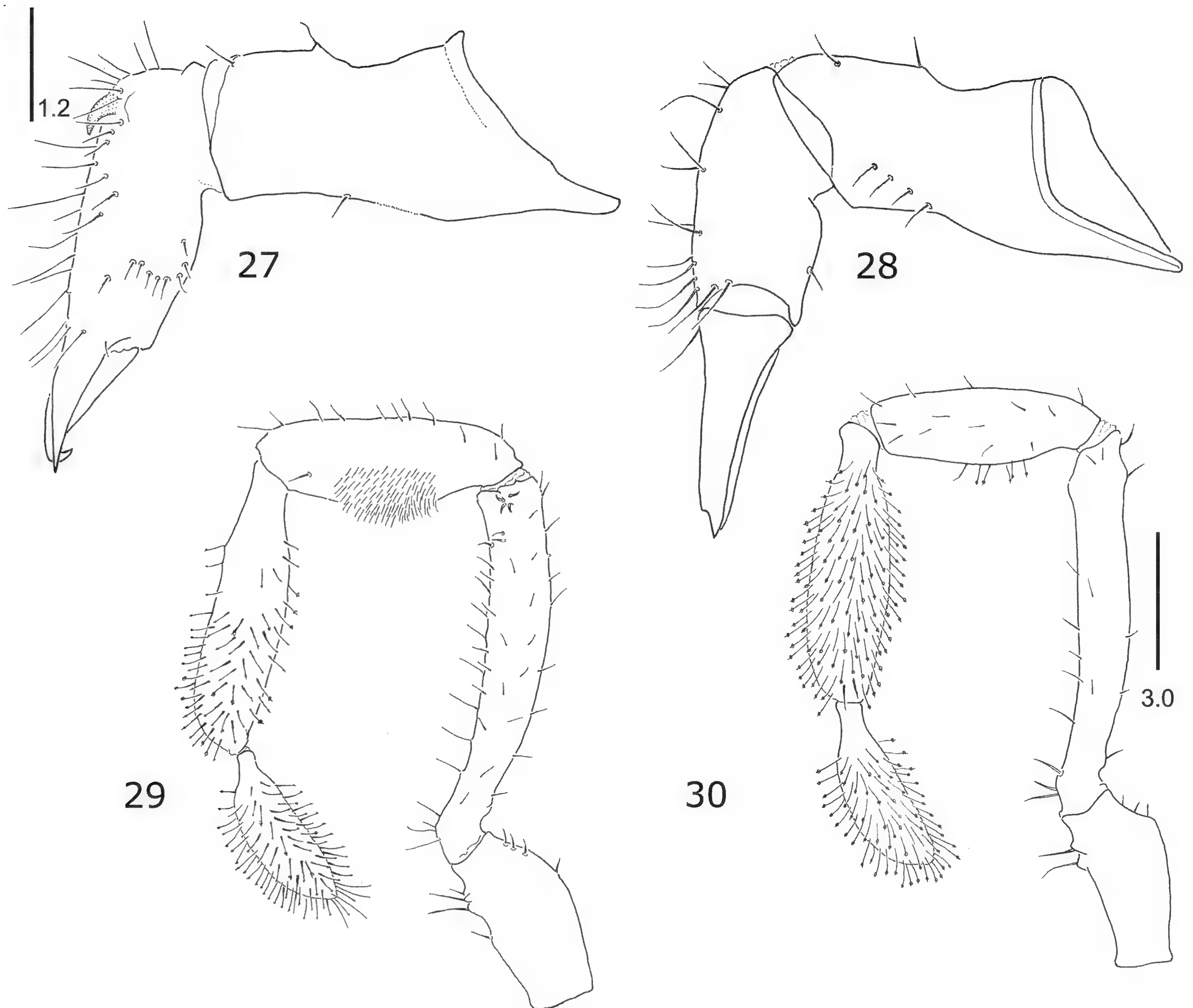
Cladolasma angka (Schwendinger & Gruber, 1992). – Shear, 2010: 17 (transfer). – Schönhofer, 2013: 24 (species listed). – Zhang & Zhang, 2013: 443 (species mentioned). – Zhang, Zhao & Zhang, 2018: 11 (species mentioned).

Material examined: MHNG; female holotype; THAILAND, Chomthong Province, Doi Inthanon

National Park, 2530 m, 28.11.1990. – 2 juvenile paratypes; same locality; 28.11.1990, 19.12.1990. – MHNG; 1 male, 10 juveniles; same locality, 2530 m; 22.2.1992. – MHNG; 1 male, decayed exoskeleton without genitalia, chelicerae and pedipalps; same locality, 2530 m; 22.2.1992. – MHNG; 2 juveniles; same locality, 2530; 13.1.1993. – MHNG, sample



Figs 20-26. *Asiolasma angka*, male. (20) Glans penis in lateral view. (21) Same in ventral view. (22) Same in dorsal view. (23) Truncus penis in ventral view. (24) Same in lateral view. (25) Prosoma in dorsal view. (26) Body in lateral view. Scales: 0.2 mm (20-22); 0.3 mm (23-24); 0.8 mm (25-26).



Figs 27-30. *Asiolasma angka*, male (27, 29), female (28, 30). (27-28) Right chelicera in prolateral view. (29-30) Right pedipalp in prolateral view. Scales: 1.2 mm (27-28); 0.3 mm (29-30).

THMA-01/15; 1 female; same locality (18°35'05.8"N, 98°28'52.3"E), lower montane forest, 2460 m; 26.12.2001. All collected by P. Schwendinger.

Remark: The species was exhaustively described based on a single female and a number of juveniles. Now also males are available and the diagnosis and description are extended accordingly.

Diagnosis: Small species with distinctly globular body; anterior part of prosoma distinctly prolonged, eye mound and projecting hood markedly elevated, rear part of eye mound and hood forming approximately a right angle with prosoma, eyes situated close to anterior margin of prosoma (la view); opisthosoma dorsally with groups of acute processes or smooth cones on areas II-IV; truncus penis straight, parallel-sided, slightly depress, spicules on glans uniform and symmetrically

arranged; male pedipalpal patella with marked proventral brush of small setae.

Description

MALE

Body shape (Figs 16, 18-19, 25-26): Distinctly globular when seen in la view (Fig. 26).

Body, dorsal side (Figs 16, 18-19, 25): Eye mound on anterior margin of prosoma distinctly elevated, projecting into distad-directed hood parallel to do body surface, hood slightly curved (la view); hood bearing one central unpaired and five la (slightly irregularly arranged) paired tubercles, sizes on left and right side different, the basic one longest, followed by a very short one, the remainder continuously prolonged towards tip of hood, all tubercles interconnected by small anvil-shaped bridges; one pair of long apophyses projecting from anterior margin of

prosoma and closely flanking hood, these apophyses longer than all hood tubercles.

Posterior margin of opisthosoma (Figs 16, 19, 26), i.e. area V, with a scattered palisade-like row of eight long and tapering tubercles of various lengths, longest in mid-part of row, between the large tubercles few smaller ones interspersed, all of them densely covered by microdenticles, all tubercles interconnected by low anvil-shaped microtubercles close to basis.

Lattice of keel cells extremely dense, forming dozens of individual cells surrounded by low anvil-shaped tubercles or keels; single larger cells situated behind Tu oc and on 1st, 2nd and 3rd opisthosomal segment laterally, in addition a row of larger cells on 5th opisthosomal segment. All anvil-shaped tubercles low and recognizable only by their light coloration contrasting with the darker cuticle surface; all large cells blackish in colour, all others light brownish. A pair of enlarged median tubercles consisting of minute thin pointed individual tubercles on scutal area II, two median pairs on area III and three pairs on area IV; all are difficult to see from above. No soil incrustation present.

Body, ventral side: Free tergites visible on ve side, each with low tubercles combined with anvil-shaped tubercles, longer tubercles interspersed; corona analis with strong tubercles as well, less so on free sternites. Front and back side of all Cx of legs with a row of tubercles each, all low and inconspicuous, on Cx I larger in front, each tubercle with low seta. Long rounded tubercles on Cx distally: I 1 retro-la, II 1 retro-la, III -, IV 1 pro-la, 1 retro-la. Massive tubercles on Tr: I 1 each pro-la and retro-la, II 1 each pro-la and retro-la, III 1 each pro-la and retro-la, IV 1 each pro-la and 1 retro-la.

Chelicera (Fig. 27): Basal article in posterior part dorsally slightly enlarged (la view), do side markedly constricted, saddle-shaped (la view), one prominent truncate tubercle with one seta on distal margin of saddle, with few setae laterally and prolaterally, no brush of setae, no obvious glandular tissue. Second article with a strong horn-like apophysis on upper side, pointed, bent downward to prolateral side. Setae of various sizes, largest ones mainly on frontal surface.

Pedipalp (Fig. 29): Tr slender, slightly swollen on do side; three small tubercles on ve side, pointed, with a strong seta each; Fe strong and massive, relatively short, continuously enlarged distally, slightly bent downwards, loosely set with few scattered normal hairs except for two groups of strong setae mediodistally; Pt slightly enlarged and bulge-like ventrally in central part, ventrally and ventro-prolaterally covered with a dense field of short setae, no apparent glandular tissue underneath; Ti cylindrical but slender, with indistinct basal stalk, not curved, with dense cover of clavate hairs concentrated in distal part; Ta more slender than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round.

Legs (Figs 16-19): All legs slightly bent ventrally. All

articles round, Fe, Pt, Ti and Ta slightly abraded, few microsetae interspersed; several indistinct white-colored noduli on Fe: in male I 3, II 6, III 3, IV 4; in female I 2, II 6, III 3, IV 4.

Genital morphology (Figs 20-24): Penis long, slender, straight, slightly depressed, almost completely parallel-sided all over its length (do/ve and la views), inconspicuously tapering towards glans, base containing pair of short muscles measuring about less than one fifth of total penis length, only slightly broader than rest of penis, deeply split into two parts (do/ve view); penis in la view slenderer than in do/ve view, parallel-sided except for slightly broadened basis, glans slightly tapering towards stylus; glans spindle-shaped and slightly broadened (only in la view), stylus short, with slight helical torsion (la view). Uniformly long, slightly spindle-like spicules and arranged into two chaplet-like groups around the glans: i) six distal spicules in symmetrically annular group on la, do and ve sides, ii) group of four proximal spicules, two of them on la side, two on ve side; no pair of proximal la spicules on distal part of truncus.

FEMALE: General characters similar to those of male; set of tubercles on posterior opisthosomal margin longer than in male (Fig. 17), eight in male, seven in female, in female distances between tubercles larger, with fewer small tubercles interspersed; ve side of female similar to that of male; chelicera (Fig. 28) similar to those of male in proportions and setation, no hook on 2nd article; pedipalp (Fig. 30) as in male, but Fe less bent, less enlarged distally, Pt only slightly enlarged, with few clavate setae ventrally; do lattice pattern similar to that of male.

Measurements: Body length of males: 3.2 (n=2), of females 3.6-3.7 (n=2). Leg II length of male, of female in parentheses: Fe 3.1 (2.9) Pt 0.8 (0.8) Ti 2.4 (2.7) Mt 1.7 (1.6) Ta 1.4 (1.3). Penis length: 1.7.

Variation: Tubercles of prosomal hood often different in length on left and right side, sometimes deformed; small tubercles on base of hood difficult to see and to count; the large apophyses on prosoma front margin projecting from hood, from margin or from either position on left and right side (observed in one specimen).

Relationships: Within *Asiolasma* the quite isolated position of *A. angka* is defined by a remarkably globular body shape, by the armament of the do side of the opisthosoma with fine peg-like tubercles (or smooth cones) concentrated in groups (Fig. 26), by the placement of the eyes on the prosoma and by a simple male genital morphology with the smallest number of spicules of all known mainland Asian species.

Distribution (Fig. 1): *Asiolasma angka* is recorded only from the Doi Inthanon National Park in northern Thailand. According to current knowledge, the species is restricted to this mountain, the highest in Thailand.

Despite numerous collecting efforts by litter and soil sieving and by setting pitfall traps by P. Schwendinger at various altitudes and in different seasons between 1990 and 2001, he was able to secure only a few juveniles and three adults, one of them a semi-decayed corpse. Apparently the species is rare and ecologically highly specialized, confined to montane forest in a narrow altitudinal corridor between 2460 m and 2530 m. Juveniles were found in XI, I and II, adults in XI and II, all outside the monsoon season when collecting activity is not hindered by constant and heavy rainfall.

***Asiolasma damingshan* (Zhang & Zhang, 2013)
comb. nov.**

Figs 1, 31, 33-46

Dendrolasma damingshan Zhang & Zhang, 2013: 444 (description of male).

Material examined: MHBUS Opi-12CZ030; male holotype; CHINA, Guangxi Autonomous Region, Wuming County, Daming Shan National Nature Reserve, 23°30'N, 108°26'E, 1231 m; Chao Zhang leg.; 18.7.2012.

Extended diagnosis: A relatively small species with slightly globular body; prolonged central anterior part of prosoma including eye mound and hood markedly elevated, eyes situated beyond anterior margin of prosoma; central and the two distal pairs of tubercles of hood longest and slender; pedipalps relatively slender, pedipalpal tibia shorter than in the geographically closest species, *A. schwendingeri* sp. nov. from Vietnam.

Description

MALE

Body, dorsal side (Figs 31, 33-34): Body rather flat but less flat than in *A. schwendingeri* sp. nov. when seen in lateral view; eye mound at anterior margin of prosoma markedly elevated, forming a rather steep ascent distinctly elevating the eyes, eye mound smooth, no tubercles on top; eyes strongly displaced distally and integrated into proximal parts of hood, central hood tubercles slightly bent downwards (la view); hood bearing one central unpaired and three lateral paired tubercles, the basic one shortest (less than half size of next one), the following ones consecutively longer, the last one nearly as long as the central unpaired one, tubercles interconnected by small anvil-shaped bridges close to their bases. Lateral to hood at each side one long and massive apophysis projecting from anterior margin of prosoma and closely flanking hood, its top reaching level between 2nd and the 3rd lateral tubercle of hood (Figs 31, 33-34). Posterior margin of opisthosoma with a row of six slender, relatively long tubercles of nearly equal length, slightly tapering towards markedly rounded tip, longest ones in mid-part of row; longer tubercles interspersed by few smaller ones,



Figs. 31-32. *Asiolasma damingshan*, male holotype (31) and *A. schwendingeri* sp. nov., male paratype (32). Body in dorsal view. Scale 1.0 mm. Photographs by P. Schwendinger.

all of them interconnected by low anvil-shaped tubercles close to base. Distinct network of large cells, each of them irregularly surrounded by anvil-shaped elevated tubercles; small and large cells on prosoma, most of them not closed; no cells on metapeltidium but a transverse row of interconnected anvil-shaped tubercles instead; on opisthosoma five rows of cells of various sizes, largest cells in mid-part near posterior margin of opisthosoma.

Body, ventral side: Front and back side of all Cx of legs with row of tubercles, on Cx I pro- and retro-la, Cx II retro-la, Cx III pro- and retro-la, Cx IV retro-la; on Cx I tubercles markedly elevated and anvil-shaped, between the rows of tubercles densely covered with pointed tubercles; Op gen, free sternites, corona analis and free tergites bent to ve side and covered with pointed tubercles, the latter with low tubercles on rough surface and scattered low setae.

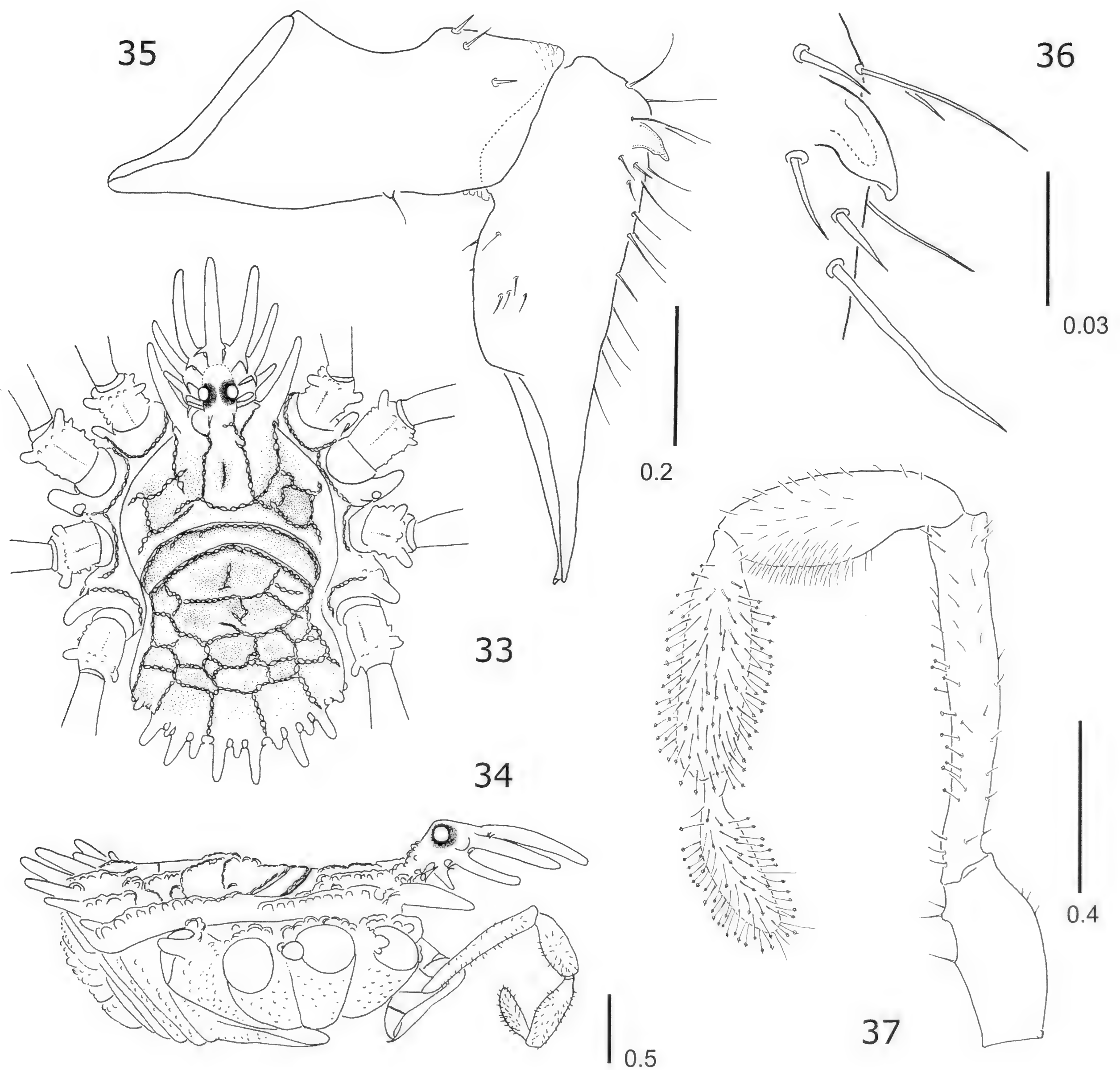
Legs: Light brownish, Mt and Ta contrastingly blackish, slender; Fe I slightly inflated, covered with densely

packed light pointed microtubercles and fine setae; long rounded tubercles on Cx: I retro-la, II 1 retro-la, III -, IV 1 pro-la; number of articles on Ta: leg I 4, II 5, III 6, IV 6. No pseudo-articulations.

Chelicera (Figs 35-36): Basal article in posterior part dorsally slightly invaginated (la view), set with few setae laterally and prolaterally, no brush of setae, no obvious glandular tissue. Second article with a strong apophysis on upper side prolaterally, pointed and slightly twisted at tip, bent downward. Setae of various sizes, mainly on frontal side.

Pedipalp (Fig. 37): Tr slender, slightly swollen on do side;

two small tubercles on ve side, pointed and with strong seta each; Fe long and slender, slightly bent downwards, slightly enlarged distally, set with few scattered setae, ventrally in proximal part with scattered clavate hairs; Pt slightly enlarged and bulge-like ventrally in distal two-thirds, ventrally and prolaterally with a loose field of short setae, no glandular tissue apparent below; Ti cylindrical but slender, with indistinct basal stalk, not curved, dense cover of clavate hairs on all sides; Ta more slender than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round, few long fine setae at distal end.

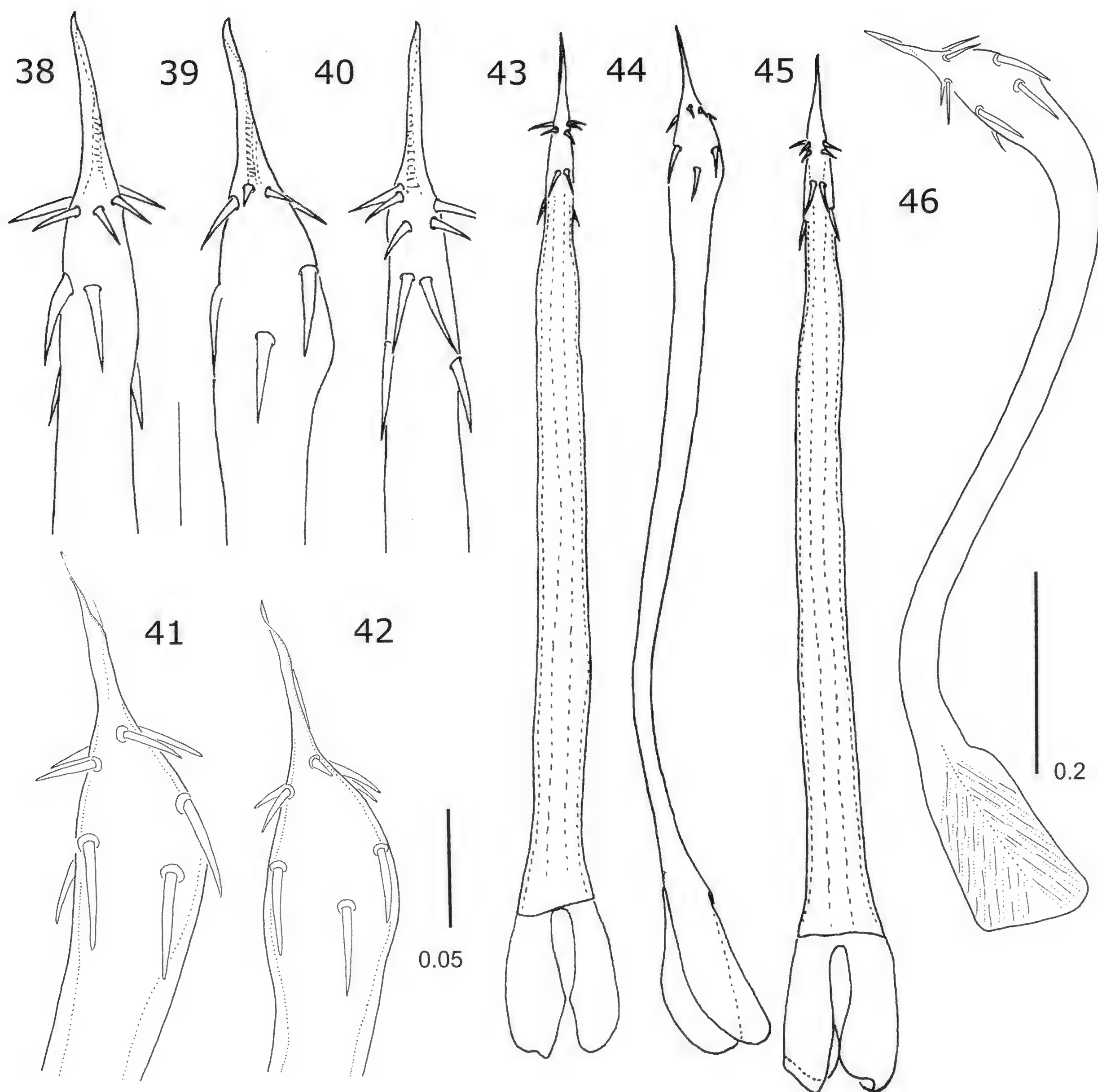


Figs 33-37. *Asiolasma damingshan*, male holotype. (33) Body in dorsal view. (34) Same in lateral view. (35) Chelicera in prolateral view. (36) Apophysis of 2nd cheliceral article in prolateral view. (37) Left pedipalp in retrolateral view. Figs 33-34 reproduced from Zhang & Zhang (2013). Scales: 0.03 mm (36); 0.2 mm (35); 0.4 (37); 0.5 mm (33-34).

Genital morphology (Figs 38-46): Penis very long and slender, about two-thirds of body length, base slightly broadened, deeply split into two parts, there two muscles concentrated; truncus moderately slender, slightly depressed, nearly parallel-sided, only slightly tapering toward distal end (ve/do view; Figs 43, 45); penis extremely slender in la view (Figs 44, 46), beyond base parallel-sided, slightly broadened below glans; glans (Figs 38-42) spindle-shaped and broadened (la view); stylus short and in strait continuation of glans, with a slight helical torsion.

Apex of penis with longer (proximal ones) or slightly shorter (distal ones) spindle-shaped spicules, these symmetrical on do and ve side and arranged in three groups from distal to proximal: i) distal group: six spicules in somewhat irregular arrangement on all sides on basis of stylus, ii) central group: four spicules, two of them on do side, the other two on la side, iii) proximal group: one each on la edge of truncus, close to and interconnected with central group of spicules (Figs 39, 42).

FEMALE: Unknown.



Figs 38-46. *Asiolasma damingshan*, male holotype. (38) Glans penis in ventral view. (39, 42) Same in lateral view. (40) Same in dorsal view. (41) Same in slightly different lateral view. (43) Whole penis in ventral view. (44, 46) Same in lateral view. (45) Same in dorsal view. Figs 38-40 and 43-45 reproduced from Zhang & Zhang (2013). Scales: 0.05 mm (38-42); 0.2 mm (43-46).

Measurements: Body length of male holotype: 3.50. Leg II: Tr 0.40, Fe 3.00, Pt 1.00, Ti 2.50, Mt 1.30, Ta 1.48 (data according to Zhang & Zhang, 2013). Penis length 1.25.

Relationships: *A. damingshan* appears closely related to *A. schwendingeri* sp. nov. from northern Vietnam (Figs 32, 88-93). Both species lack a massive cheliceral apophysis on 1st cheliceral article; body size in *A. damingshan* (Fig. 31) smaller, tubercle of anterior hood (absolutely and relatively) shorter, slenderer, thus forming a narrower palmate fan cover above pedipalps and chelicerae than in *A. schwendingeri* sp. nov. Pedipalpal tibia is shorter and slenderer than in the latter species. Armature of glans differs, two proximal spicules in *A. schwendingeri* sp. nov. are more remote from central group of spicules (Figs 38-42 cf. Figs 94-96).

Distribution (Fig. 1): This species is so far only known from a locality in the Daming Shan Natural Reserve in the Chinese province Guangxi. The sole specimen was collected from soil litter in a subtropical rain forest at 1231 m altitude (Zhang & Zhang, 2013).

***Asiolasma ailaoshan* (Zhang, Zhao & Zhang, 2018)
comb. nov.**

Figs 1, 47-59

Cladolasma ailaoshan Zhang, Zhao & Zhang, 2018: 12 (description of male and female).

Material examined: MHBU Opi-20160422; male holotype; CHINA, Yunnan Province, Zhenyuan County, Qianjiazai town, Daming Shan, Ailao Shan Natural Reserve, 24°16'12"N, 101°15'46"E, 2170 m; A. Nakamura leg.; 18.8.2011. – MHBU Opi-20160423; female paratype; collected together with holotype.

Diagnosis: Body rather globular, prolonged anterior part of prosoma including eye mound and hood slightly elevated, distal part of hood slightly bent downward, tubercles of hood markedly fanned, massive apophyses on anterior margin of prosoma flanking hood laterally; marked sexual dimorphism in body size, female much larger than male.

Description

MALE

Body, dorsal side (Fig. 53): Body rather flat but less flat than in *A. schwendingeri* sp. nov. when seen in la view (Fig. 54); Tu oc at anterior margin of prosoma only slightly elevated and forming no marked bend, eyes not distinctly raised on tubercle, displaced beyond anterior margin of prosoma and integrated into proximal part of hood, central hood tubercle slightly bent downwards (la view); hood bearing one central unpaired and four lateral paired tubercles, proximal pair shortest (about half size of following one), next two pairs consecutively longer,

last pair nearly as long as central unpaired tubercle; all hood tubercles interconnected by small anvil-shaped bridges close to their bases. Lateral to hood one long and massive apophysis on each side projecting from anterior margin of prosoma, slightly bent inwards and flanking hood, distinctly shorter than all other appendages in prosoma front area.

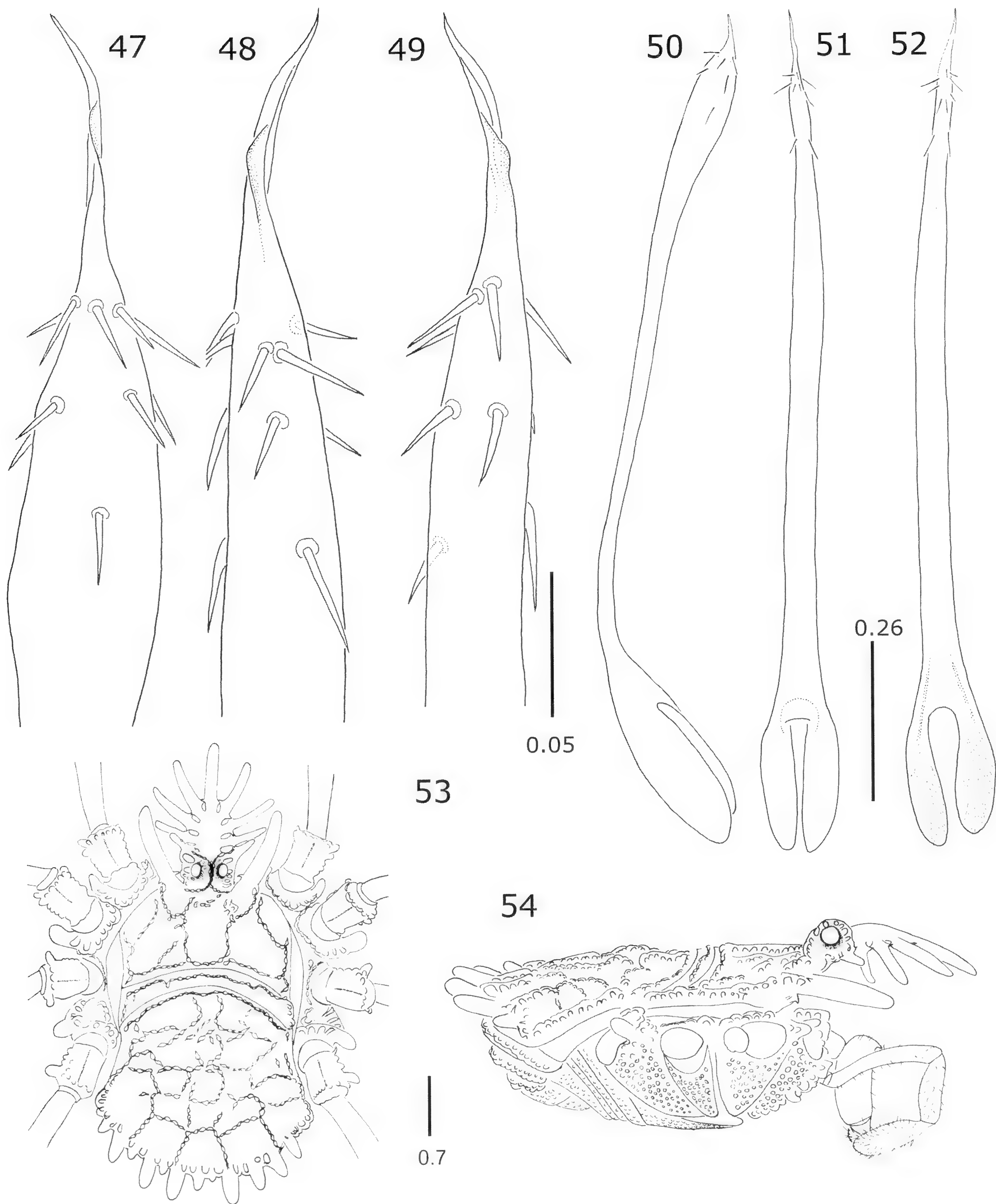
Posterior margin of opisthosoma with a row of six massive truncate tubercles slightly tapering towards rounded tip, longest in mid-part of row (Fig. 53). Network of keel cells loose, most cells not closed and interconnected with neighbouring ones; three large central cells on prosoma, two additional small ones on disto-lateral margin of prosoma; on metapeltidium no cells but a transverse row of anvil-shaped tubercles all over its breadth; on opisthosoma irregular open cells of different sizes, the five largest ones opening towards posterior end of opisthosoma.

Ventral side: Coxae densely set with small setae-bearing tubercles on ventral surfaces and with dorso-distal rows of anvil-shaped tubercles; a row of anvil-shaped tubercles along anterior and posterior margins of coxae II-IV; coxae I and II with distal digitiform processes retrolaterally; coxa IV with similar process prolaterally. Genital operculum short, almost tongue-shaped, surface with irregular tubercles. Sternites with transverse rows of low keels, reduced along midline.

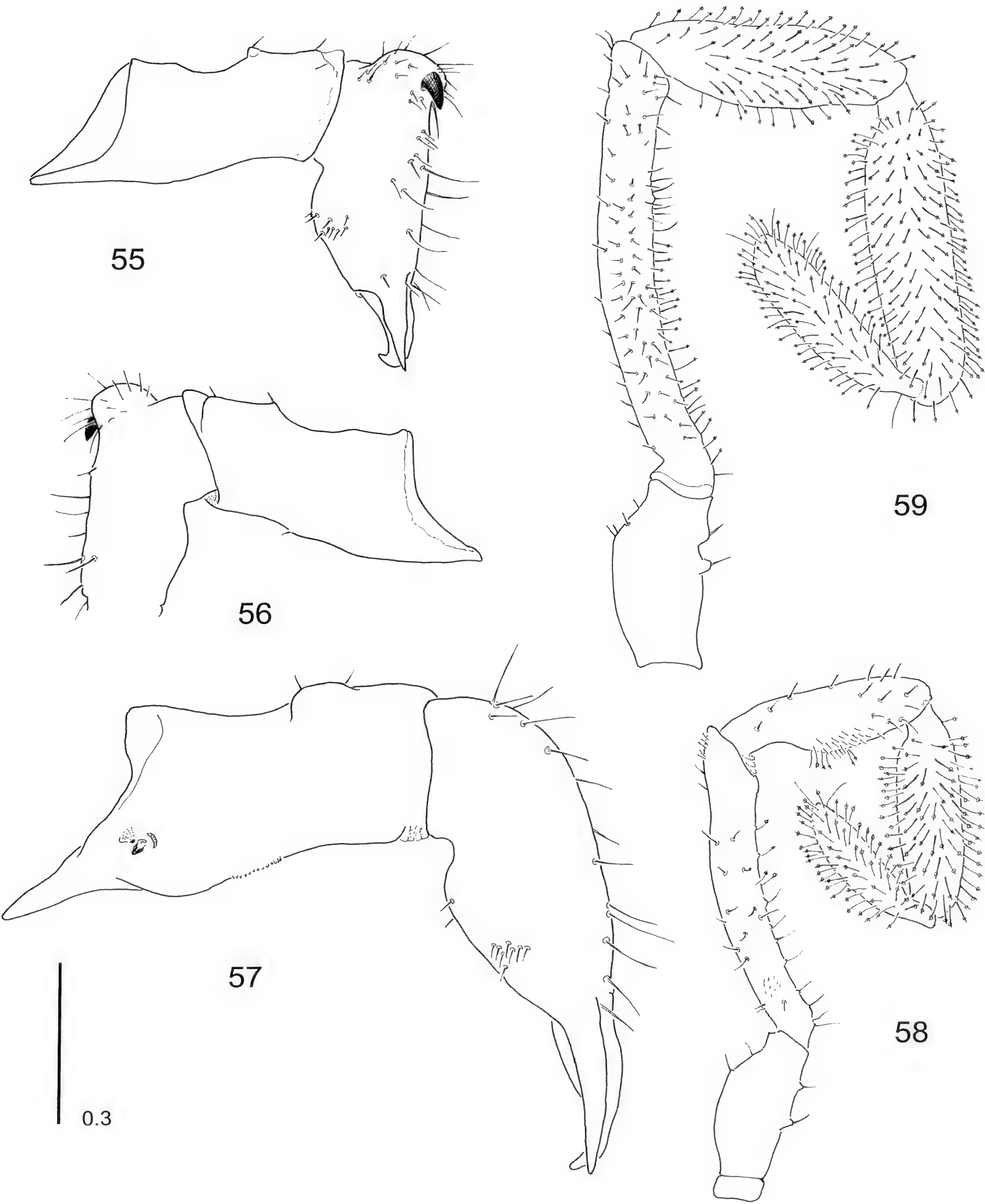
Chelicera (Figs 55-56): Basal article in posterior part dorsally slightly invaginated (la view), in distal part a low apophysis set with a short seta; 2nd article with a massive rounded apophysis on upper side carrying a pointed hook directed downwards and running more or less parallel to front of 2nd article; setae of various sizes, longest on frontal surface, few setae laterally and prolaterally, no brush of setae, no obvious subcuticular glandular tissue.

Pedipalp (Fig. 58): Tr slender, slightly swollen on do side; two small tubercles on ve side, each one pointed and with a small seta; Fe long and slender, slightly bent downwards, slightly enlarged distally, set with few scattered setae, ventrally with scattered clavate hairs, few of those distally; Pt with basal stalk, slightly enlarged and bulge-like ventrally, with a loose field of short setae and only five clavate setae, no apparent glandular tissue below; Ti cylindrical and moderately slender, with indistinct basal stalk, not curved, dense cover of clavate hairs on all sides; Ta slenderer than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round, few longer normal setae at distal end.

Genital morphology (Figs 47-52): Penis very long and slender, slightly more than two-thirds of body length, slightly depressed (do/ve view), basis broadened, deeply split into two parts, two muscles concentrated there, from basis slightly tapering towards apex, then parallel-sided up to tip including glans (do/ve view); glans spindle-shaped and broadened (la view); stylus short and in straight continuation of glans, with a slight helical torsion. Armature consisting of uniformly long (proximal



Figs 47-54. *Asiolasma ailaoshan*, male holotype. (47) Glans penis in lateral view. (48) Same in dorsal view. (49) Same in ventral view. (50) Truncus penis in lateral view. (51) Same in ventral view. (52) Same in dorsal view. (53) Body in dorsal view. (54) Same in lateral view. Figs 47-48 reproduced from Zhang *et al.* (2018). Scales: 0.05 mm (47-49); 0.26 mm (50-52); 0.70 mm (53-54).



Figs 55-59. *Asiolasma ailaoshan*, male (55-56, 58), female (57, 59). (55, 57) Right chelicera in prolateral view. (56) Same in retrolateral view. (58-59) Left pedipalp in prolateral view. Scale: 0.3 mm.

ones) or shorter (distal ones) spindle-shaped spicules, these symmetrical on do and ve side and arranged in three groups from distal to proximal: i) distal group: six spicules in somewhat irregular arrangement, ii) central group: four spicules mainly situated on do and la sides in annular arrangement, iii) proximal group: two spicules distinctly separated from central group on la edges of truncus, one each on la side.

FEMALE: Body much larger than in male; chelicera (Fig. 57) without apophysis on 1st article, generally more slender but much larger than in male; pedipalp (Fig. 59) much larger than in male, general appearance as in male, its Pt less bulged in ve view.

Measurements: Body length of male: 2.8 (n=1), of female 4.6 (n=1). Leg II length of male, of female in parentheses: Fe 2.68 (4.49), Pt 0.88 (1.21), Ti 2.37 (4.09), Mt 1.53 (1.94), Ta 1.33 (1.58) (data according to Zhang *et al.*, 2018). Penis length in strongly curved state 1.05.

Relationships: *Asiolasma ailaoshan* appears closely related to *A. juergengruberi* sp. nov. The latter is much larger (3.0-3.4 mm for male and female) than *A. ailaoshan*. *Asiolasma ailaoshan* is sexually dimorph, the female being much larger than the male (2.8 mm in male, 4.6 mm in female), the apophysis of the male 2nd cheliceral article is less high, more flat, its pointed thorn is directed more downwards and runs parallel to the front side of the article; the proximal pair of spicules of the glans penis is slightly closer to the mid-group spicules than in *A. juergengruberi* sp. nov.

Distribution (Fig. 1): At present this species is only known from the Ailao Shan Natural Reserve in the Chinese province of Yunnan. The two specimens were collected from soil litter in a (sub)tropical rain forest at 2170 m altitude (Zhang *et al.*, 2018).

***Asiolasma juergengruberi* sp. nov.**

Figs 1, 60-87

Holotype: SMF; male; CHINA, northern Yunnan Province, southwest of Lugu Hu (lake), patch of primeval broadleaf forest mixed with scattered pine trees along a road, 3300 m, 27°37' N, 100°49'E; J. Martens leg.; 28.5.2011.

Paratypes: CJM 8143; 1 male, 2 females; collected together with the holotype. – CJM 8144; 2 males; CHINA, northern part of Yunnan Province, Lijiang Naxi, Autonomous County, E of Yulongxue Shan, 30 km N of Lijiang, 2800-2900 m, creek valley, secondary mixed broad leaf and coniferous forest, 27°09.0'N, 100°14.9'E; D.W. Wrase leg.; 13.8.2003.

Diagnosis: A medium-sized, rather globular species with flat Tu oc and hood and with relatively short hood projection; 2nd cheliceral article with pointed hook on

broad elevated apophysis. Penis shaft extremely slender, with short enlarged base, glans/truncus armature containing two proximally dislocated lateral spicules.

Name: This species is dedicated to Dr Jürgen Gruber, an esteemed arachnologist who, together with W.A. Shear, has meticulously studied American and Asian ortholasmatine harvestmen. Name in genitive case.

Description

MALE

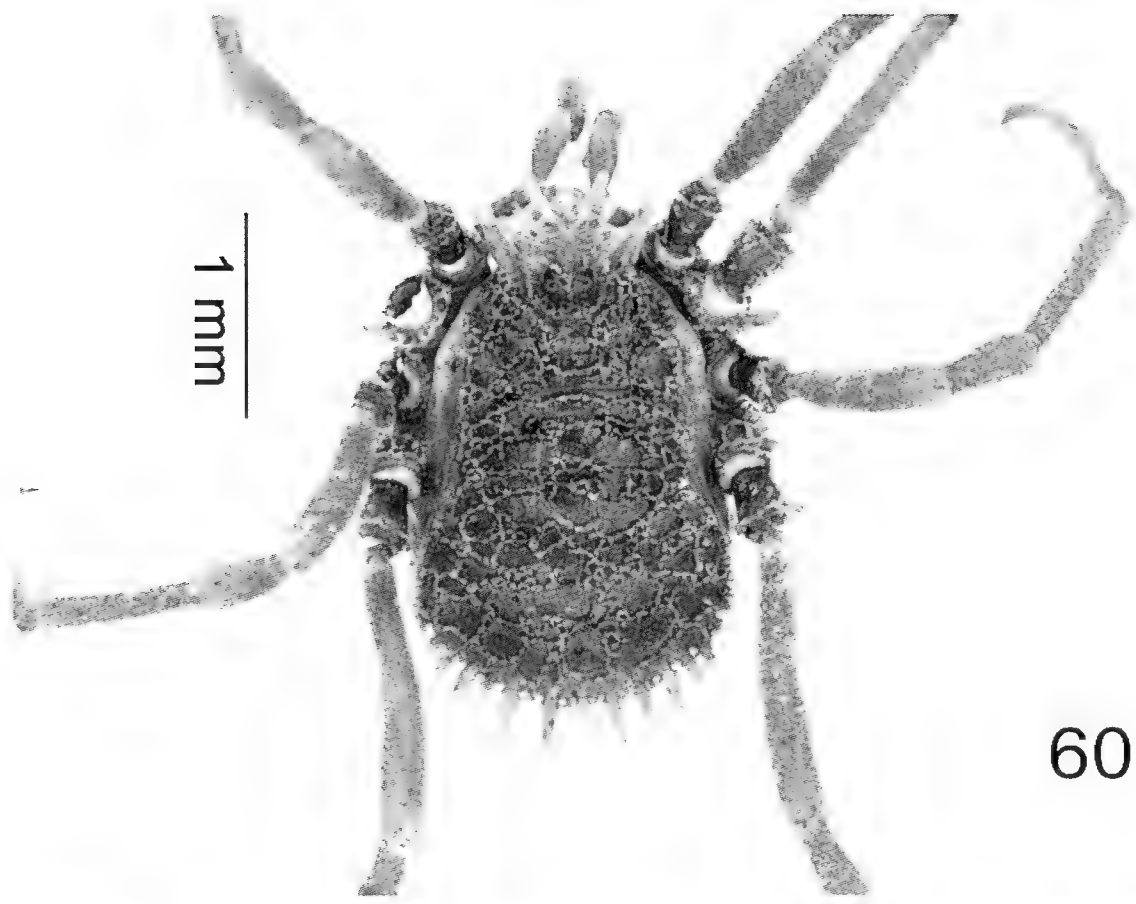
Body, dorsal side (Figs 60, 62-63, 65-66): Body dark, nearly black, with dark bluish tinge, slightly elongated (do view), distinctly globular (la view); eye mound on anterior margin of prosoma rather flat and only slightly elevated, projecting into distad-directed hood forming an obtuse angle with do body surface (la view); hood flat, relatively short, bearing one central unpaired and four lateral paired tubercles, the basal one minute and shortest (difficult to see), the distad ones consecutively longer, these tubercles interconnected by robust anvil-shaped bridges in lower half of tubercles. On each side of hood two long apophyses projecting from anterior margin of prosoma and closely flanking hood, the outer ones longer and more massive than the inner ones; all apophyses and tubercles covered by a coat of fine micro tubercles all round.

Posterior margin of opisthosoma (Figs 60, 63, 65) with a row of 12 long and pointed tubercles of various lengths tapering to narrowly ending tip, longest ones in mid-part of row; at bases tubercles interconnected by low anvil-shaped tubercles forming small basal “windows” (Figs 60, 63); dense coat of microtubercles and few short setae all round.

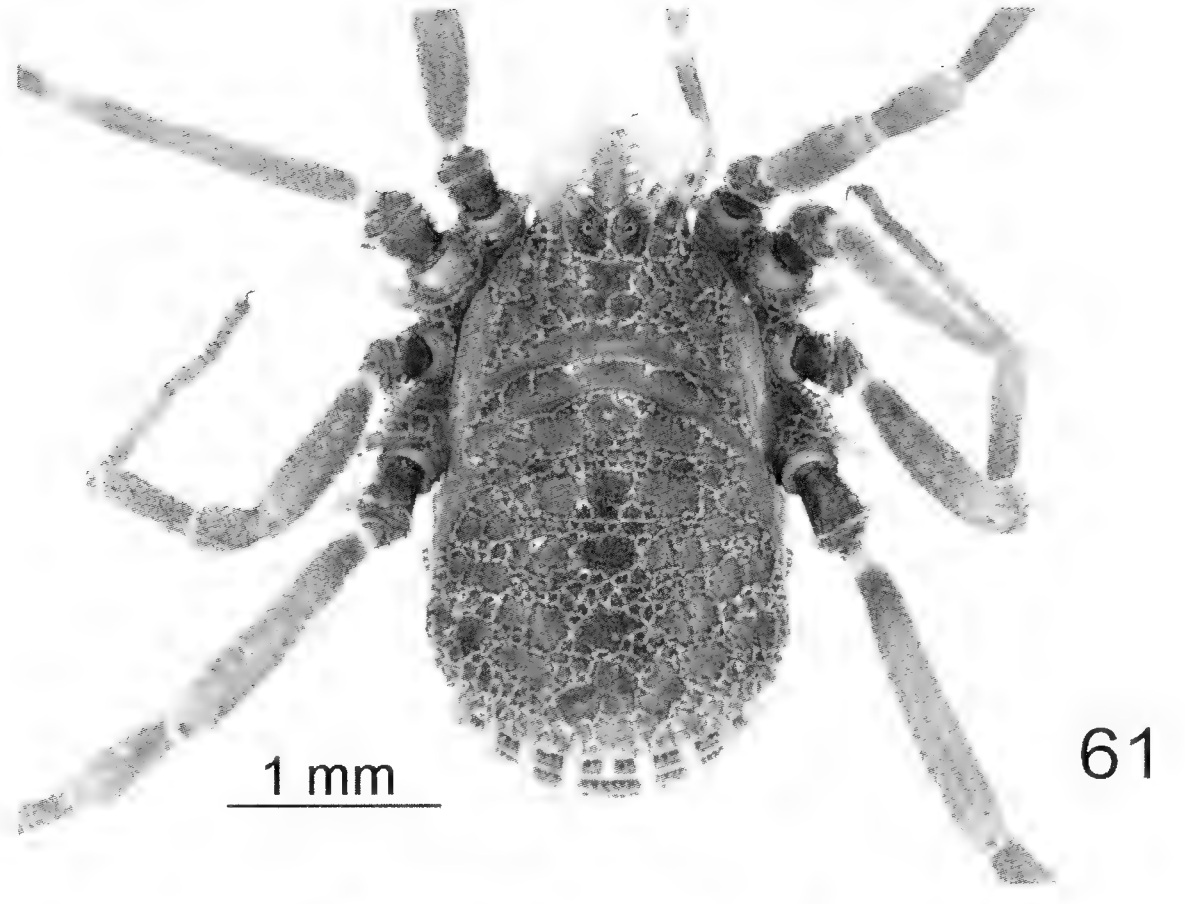
Network of prosomal and opisthosomal keel cells formed by light yellowish anvil-shaped tubercles contrasting with dark smooth cuticle (Figs 60-64); low, well developed, slightly elevated anvil-shaped tubercles (these stronger than in other Asian species) forming many individual small, often open cells all over prosoma, a large one behind Tu oc, on metapeltidium only two minute cells laterally and a row of tubercles on anterior margin; on opisthosoma larger cells in irregular arrangement and of different sizes, largest ones in a para-median row from anterior to posterior and near posterior margin of opisthosoma, in central part and on lateral margin most cells small, only a central large one, always surrounded by low anvil-shaped tubercles.

Body, ventral side: Only on Cx I an indistinct row of large tubercles; other Cx and Op gen with low tubercles, very few of them on free sternites, these bent to ve side, entire ve side with fine incrustation of minute mineral particles. Long, distally rounded tubercles on Cx: I -, II 1 retro-la, III -, IV 1 pro-la. Tubercles on Tr: I 1 very small pro-la and 1 retro-la, II 2 small retro-la, III 1 pro-la, 2 small retro-la, IV 1 pro-la.

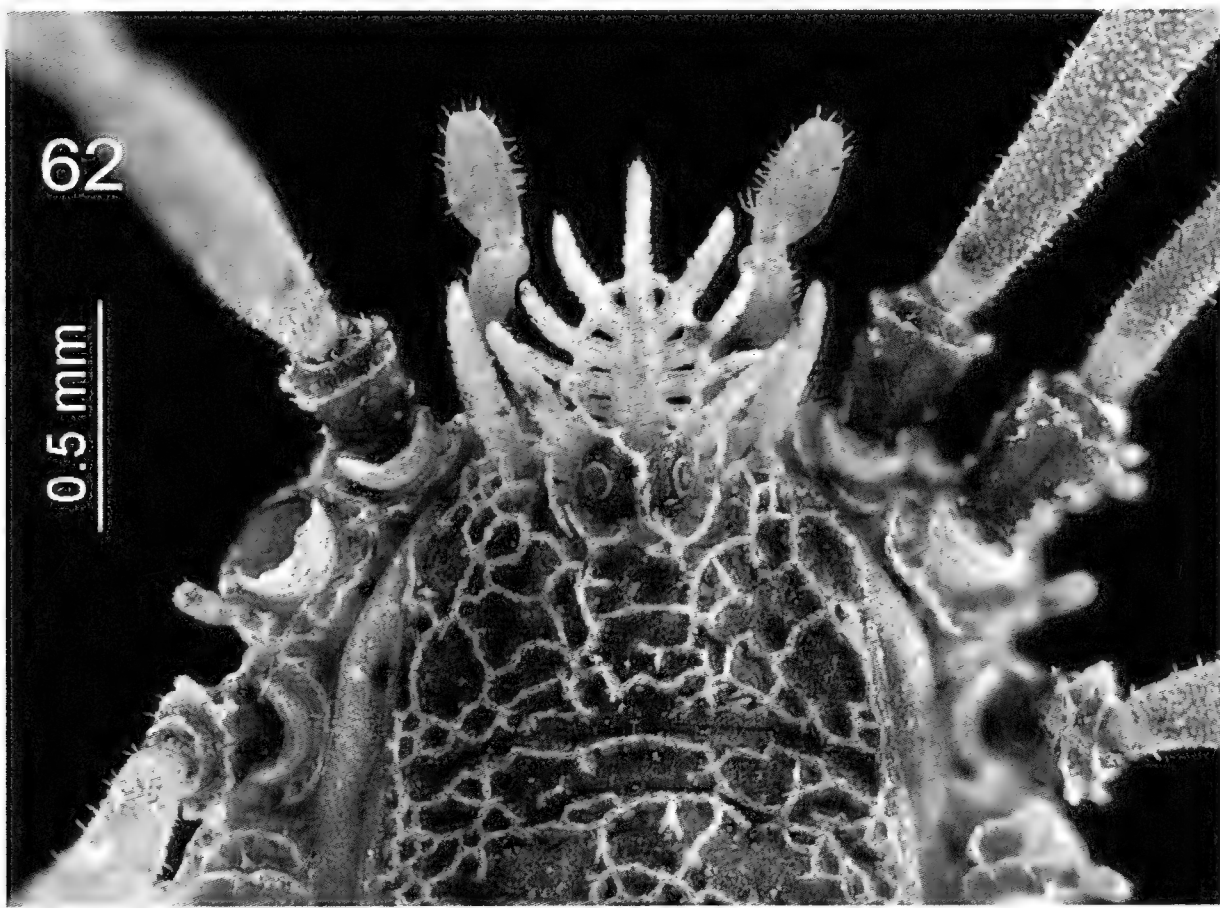
Chelicera (Figs 72-75, 77): Basal article on do side with a large, hornlike apophysis slightly bent forward, article



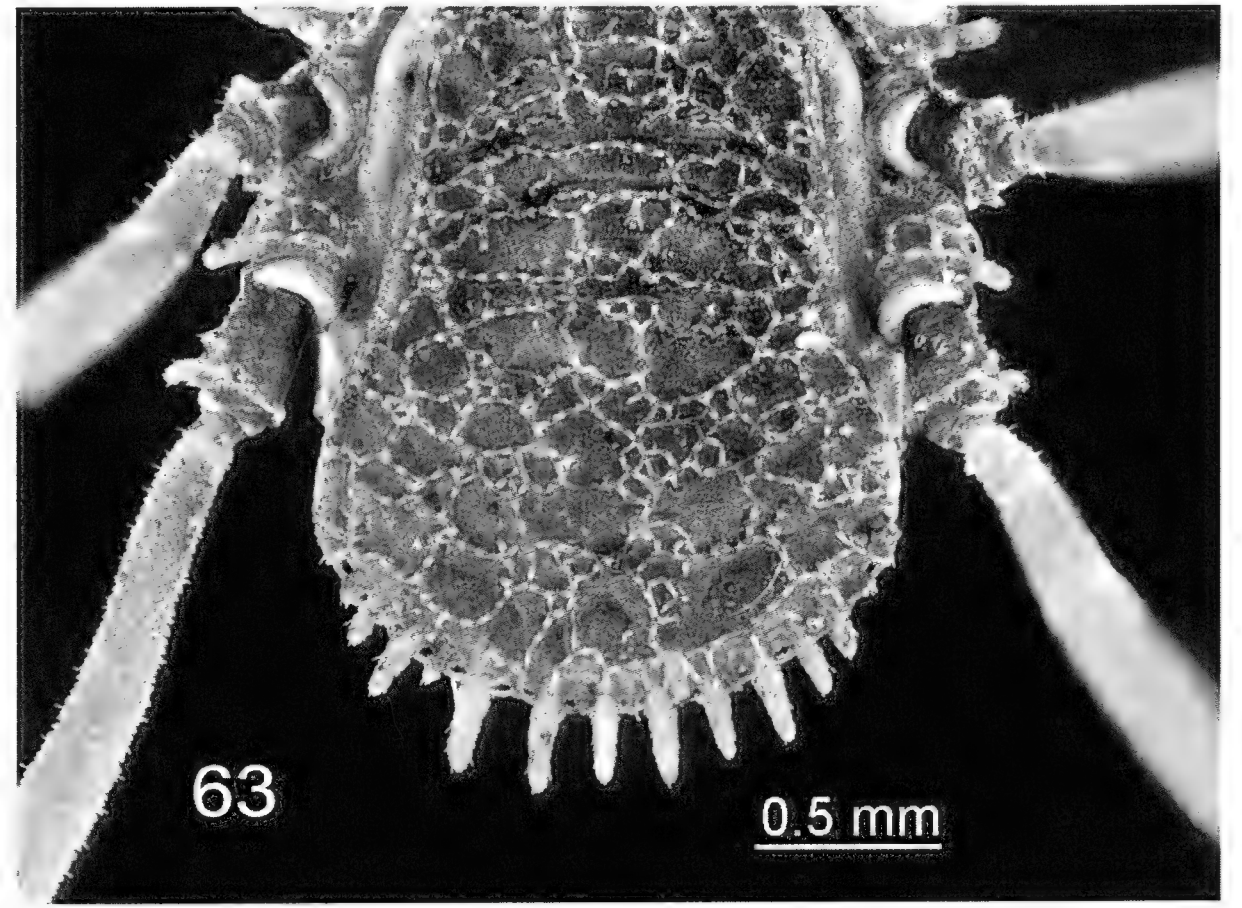
60



61



62



63

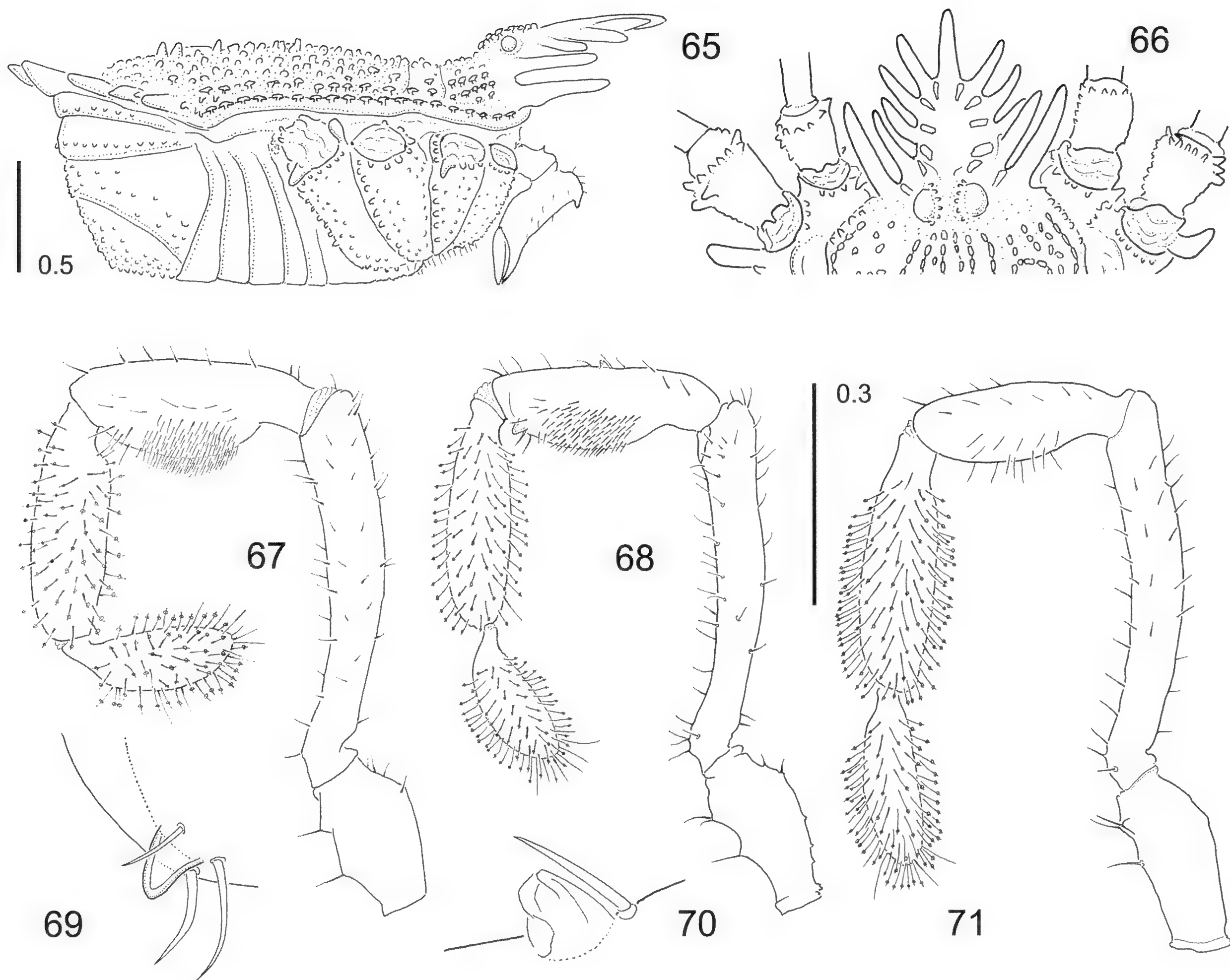
0.5 mm



64

0.5 mm

Figs 60-64. *Asiolasma juergengruberi* sp. nov., male (60, 62-63), female (61, 64). (60-61) Whole body in dorsal view. (62, 64) Prosoma in dorsal view. (63) Opisthosoma in dorsal view. Photographs by J. Schmidt.



Figs 65-71. *Asiolasma juergengruberi* sp. nov., male (65-70), female (71); specimens from Lugu Hu (65-67, 71), specimen from Lijiang area (68-70). (65) Body in lateral view. (66) Prosoma dorsal view. (67-68, 71) Right pedipalp in prolateral view. (69) Apophysis ventrodistally on patella. (70) Same dorsally. Scales: 0.03 mm (67-68, 71); 0.5 mm (65-66); no scale (69-70).

set with few setae laterally and prolaterally, ventrally a row of minute setae, no obvious glandular tissue. Second article on upper side with a large bipartite apophysis with a broad and massive basis extended into a sickle-like pointed apophysis bent forward and slightly to prolateral side. A small field of minute tubercles at basis of sickle-like part of apophysis, best seen from prolateral side.

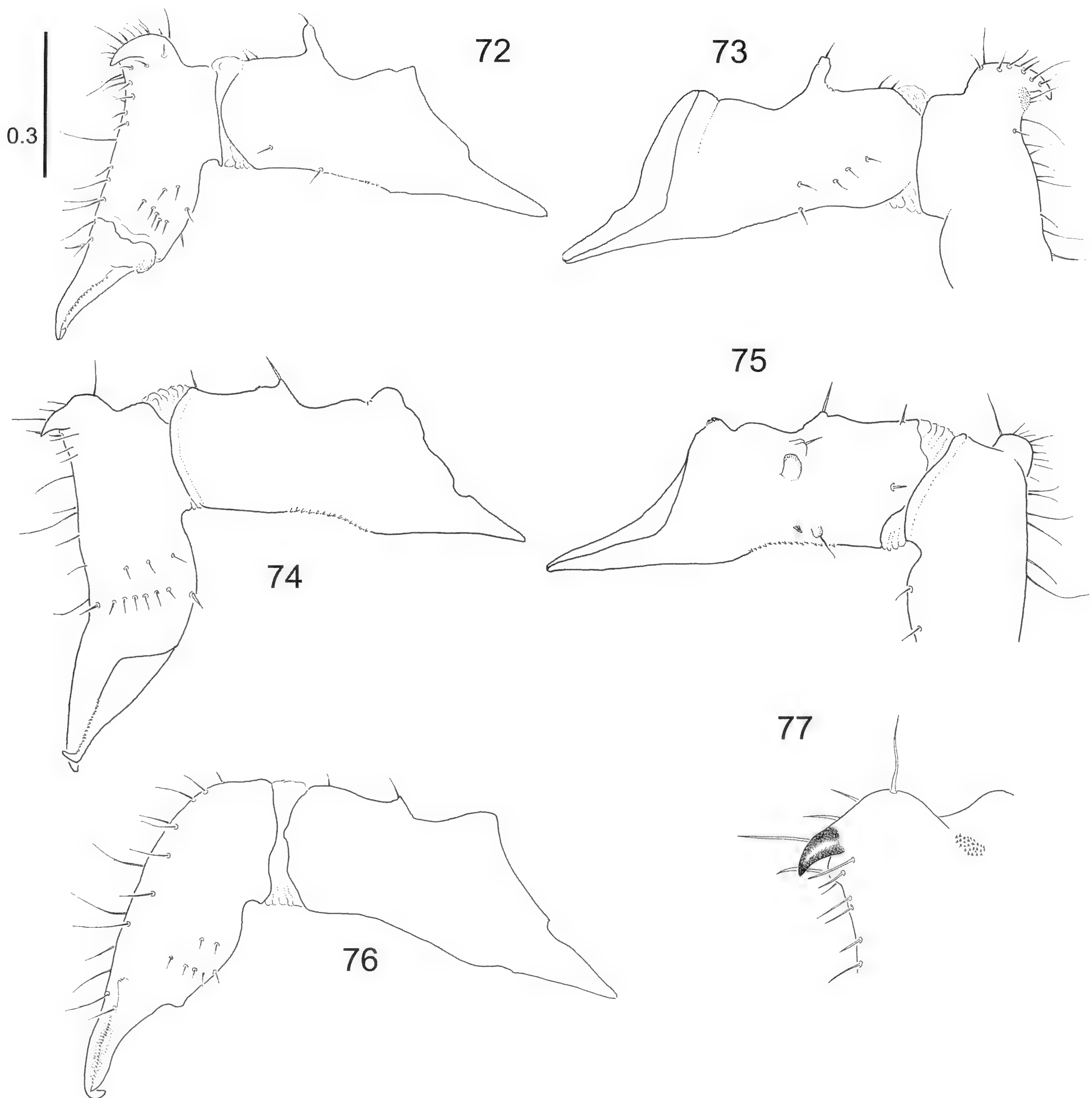
Pedipalp (Figs 67-70): Tr slender, slightly swollen on do side, ventrally with two low tubercles carrying a seta each; Fe slender, slightly club-shaped, bent ventrally and enlarged distally, set with few scattered normal hairs, no clavate hairs; Pt strongly bulge-like and enlarged ventrally, covered ventrally and prolaterally with a field of short setae with glandular tissue below, otherwise few scattered setae on all sides; Ti cylindrical and moderately thick, with basal stalk, inconspicuously curved, clavate hairs on all sides; Ta oval, stalked, slightly inflated on do side, covered with clavate setae all round.

Legs (Figs 60, 62-63): Short, robust, dark brown to

blackish; Fe I and III slightly inflated, covered with minute fine texture of microtubercles and interspersed with minute setae; no pseudo-articulations.

Genital morphology (Figs 78-87): Penis very long and slender, more than two-thirds of body length, basis broadened, deeply split into two parts, two muscles concentrated there; penis above basis slender, parallel-sided (ve/do and la views); glans parallel-sided in do/ve view, slightly tapering toward stylus (do/ve view), spindle-shaped and broadened in la view; stylus short, with a slight helical torsion. Armature with long uniform spindle-shaped spicules, symmetrical on do and ve side and arranged in three groups, these from distal to proximal position: i) six spicules: two each on ve and do side, one on each la side (the latter longest), ii) four, two of them on ve and two on do side, and iii) two spicules on each la sides, the latter on distal part of truncus and distinctly separated from groups i and ii.

FEMALE: Chelicera (Fig. 76) as in male, but do



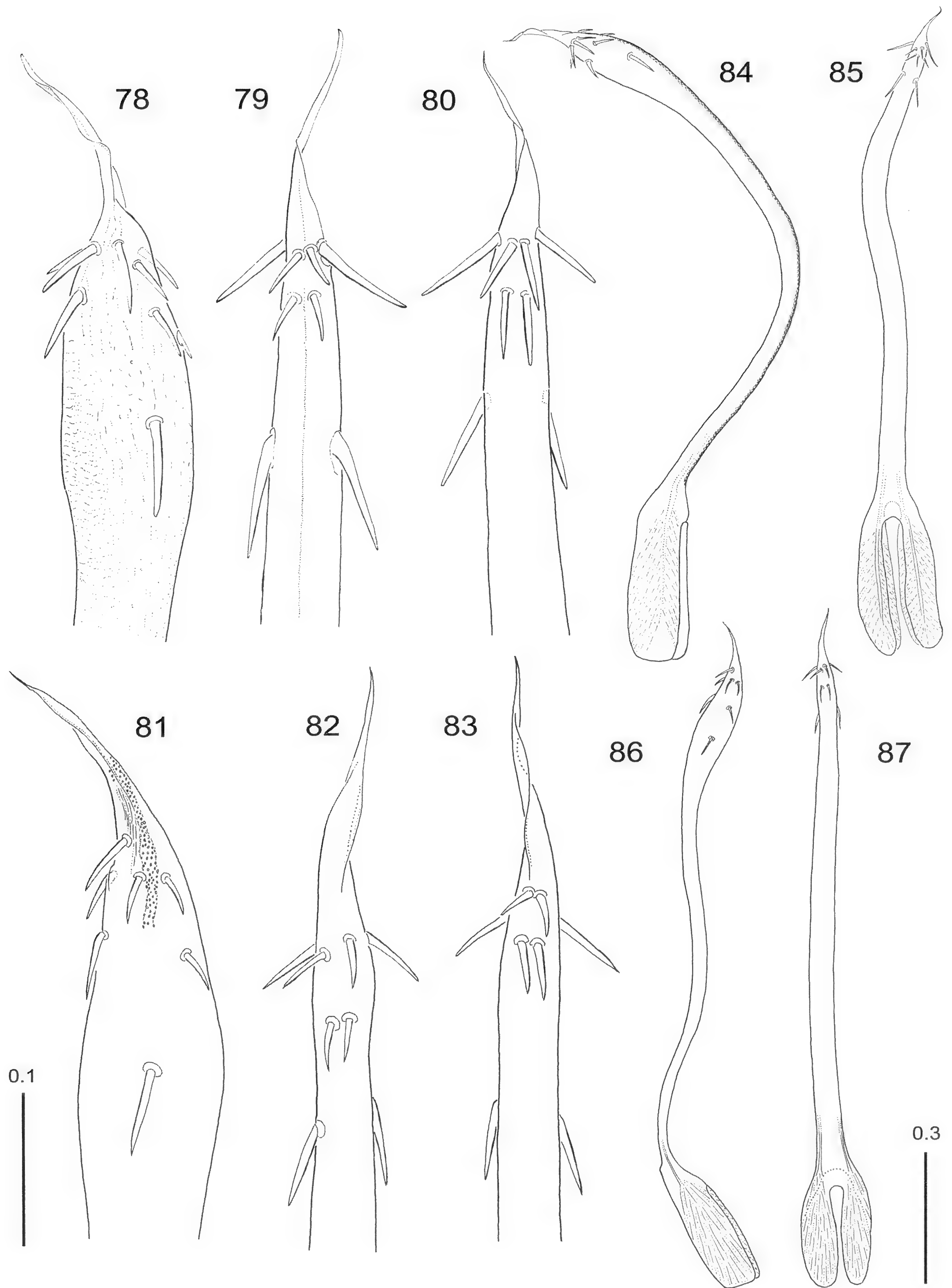
Figs 72-77. *Asiolasma juergengruberi* sp. nov.; male (72-75, 77), female (76). (72, 74, 76) Right chelicera in prolateral view. (73, 75) Same in retrolateral view. (77) Apophysis of 1st cheliceral article. (72-73, 76-77) specimen from Lugu Hu. (74-75) specimen from Lijiang. Scale: 0.3 mm (72-76); no scale (77).

apophysis on basal article smaller, no apophysis on 2nd article; pedipalp (Fig. 71) as in male, but Pt less inflated, no brush of setae on medio-ventral side, only with a few scattered longer setae; keel network on do side of body slightly different (Figs 61, 64), also among specimens; on metapeltidium only one keel cell laterally; nine tubercles on posterior margin of opisthosoma, these shorter than in male and thus more massive.

Measurements: Body length of males 3.0-3.3 (n=3), of females 3.2-3.4 (n=2). Leg II of male, of female in

parentheses: Fe 2.3 (2.2), Pt 0.8 (0.8), Ti 1.9 (1.8), Mt 1.7 (1.6), Ta 1.5 (1.3). Penis length 1.7.

Variation: In specimens from the Lijiang area of Yunnan the basal article of the chelicera has on its do side a slightly smaller hornlike apophysis than in the specimens from Lugu Hu, and the do hook on the 2nd article is lower, less prominent. The differences between the cheliceral hooks visible in Figs 73 and 75 are due to different angles of view. Little variation was observed in penis morphology; the penis of the Lijiang



Figs 78-87. *Asiolasma juergengruberi* sp. nov., genital morphology of male from Lugu Hu (78-80, 84-85) and of male from Lijiang (81-83, 86-87). (78, 81) Glans penis in lateral view. (79, 82) Same in ventral view. (80, 83) Same in dorsal view. (84, 86) Whole penis in lateral view. (85, 87) Same in dorsal view. In Fig. 81 subdistal opening of sperm duct is indicated, end of sperm duct is filled with sperm. Scales: 0.1 mm (78-83); 0.3 mm (84-87).

specimen appears slenderer than the penes of the Lugu Lake specimens (la view), it is narrowest above base, then continuously but slightly widens towards glans. The armature of glans in the Lijiang male examined is as in the Lugu Lake specimens, but the spicules of group i are slightly irregular (Figs 81-83). The pedipalp of the Lijiang specimen is with a small rounded apico-prolateral apophysis and with a smaller truncate apophysis on the do side of the Pt (Figs 68-70), which lack in other males examined.

Relationships: With respect to male genital morphology, *A. juergengruberi* sp. nov. is closest to *A. billsheari* sp. nov. In both species the penial spicules of groups ii and iii are widely separated, and the latter ones are situated in the distal part of the truncus. Both species have in common that the hook of the 2nd cheliceral article is placed on a solid elevated apophysis. The latter character is present also in the tropical species *A. ailaoshan*, though being less prominent there. The prosomal hood is short in *A. juergengruberi* sp. nov. and *A. billsheari* sp. nov.; in *A. ailaoshan* it is considerably longer.

Distribution (Fig. 1): According to present information, the species is confined to mountainous areas in northern Yunnan, China. The two localities known to date, Lugu Lake and close to Lijiang, are about 70 km apart in NE-SW direction. Primeval mixed broadleaf and coniferous forests prevail there. The localities are at 3300 m (Lugu Hu) and 2800-2900 m (Lijiang area) altitude.

Asiolasma schwendingeri sp. nov.

Figs 1, 32, 88-103

Holotype: MHNG; male; VIETNAM, Ha Noi Province, Ba Vi District, Mt Ba Vi (21°04'12"N, 105°21'55"E), 900 m, evergreen forest; A. Schulz leg.; 17.5.2012 [sample VN-12/17].

Paratypes: MHNG, 2 males, 2 females; CJM 8145, 1 male, Mt Ba Vi (21°03'35"N, 105°22'02"E), 1000-1070 m, evergreen forest; P. Schwendinger & A. Schulz leg.; 16.-18.5.2012 [sample VN-12/05c].

Non-types: MHNG; 2 juveniles; Mt Ba Vi (21°03'35"N, 105°22'02"E), 1000-1070 m, evergreen forest; P. Schwendinger & A. Schulz leg.; 16.-18.5.2012 [sample VN-12/05c].

Diagnosis: Largest and most long-legged of all *Asiolasma* species, with rather flat body, anterior part of prosoma including eye mound and hood slightly elevated (la view), visual impression of body massive caused by short hood but slender and fanned tubercles of hood (Figs 88-93); conspicuously long and slender pedipalps only in this species; pedipalpal tibia and tarsus together longer than femur (in both sexes).

Name: The species is dedicated to Dr Peter Schwendinger, esteemed arachnologist, who extensively collected arachnids in Southeast Asia, including specimens of this species and of *A. angka*. Name in genitive case.

Description

MALE

Body, dorsal side (Figs 88-89, 91-93): Body (Fig. 92) rather flat when seen in la view; Tu oc on anterior margin of prosoma markedly elevated and continuing into short hood; central and distal tubercles of hood parallel to surface of prosoma (la view); hood bearing one central unpaired and three lateral paired tubercles, the basic one shortest, the following ones consecutively longer, the unpaired one longest, all neighbouring ones interconnected by small anvil-shaped bridges close to their bases; tubercles slender, markedly spread, forming an open symmetric palmate fan; on each side of hood one long apophysis projecting from anterior margin of prosoma and closely flanking hood, its tip on a level between 2nd and 3rd tubercle of hood.

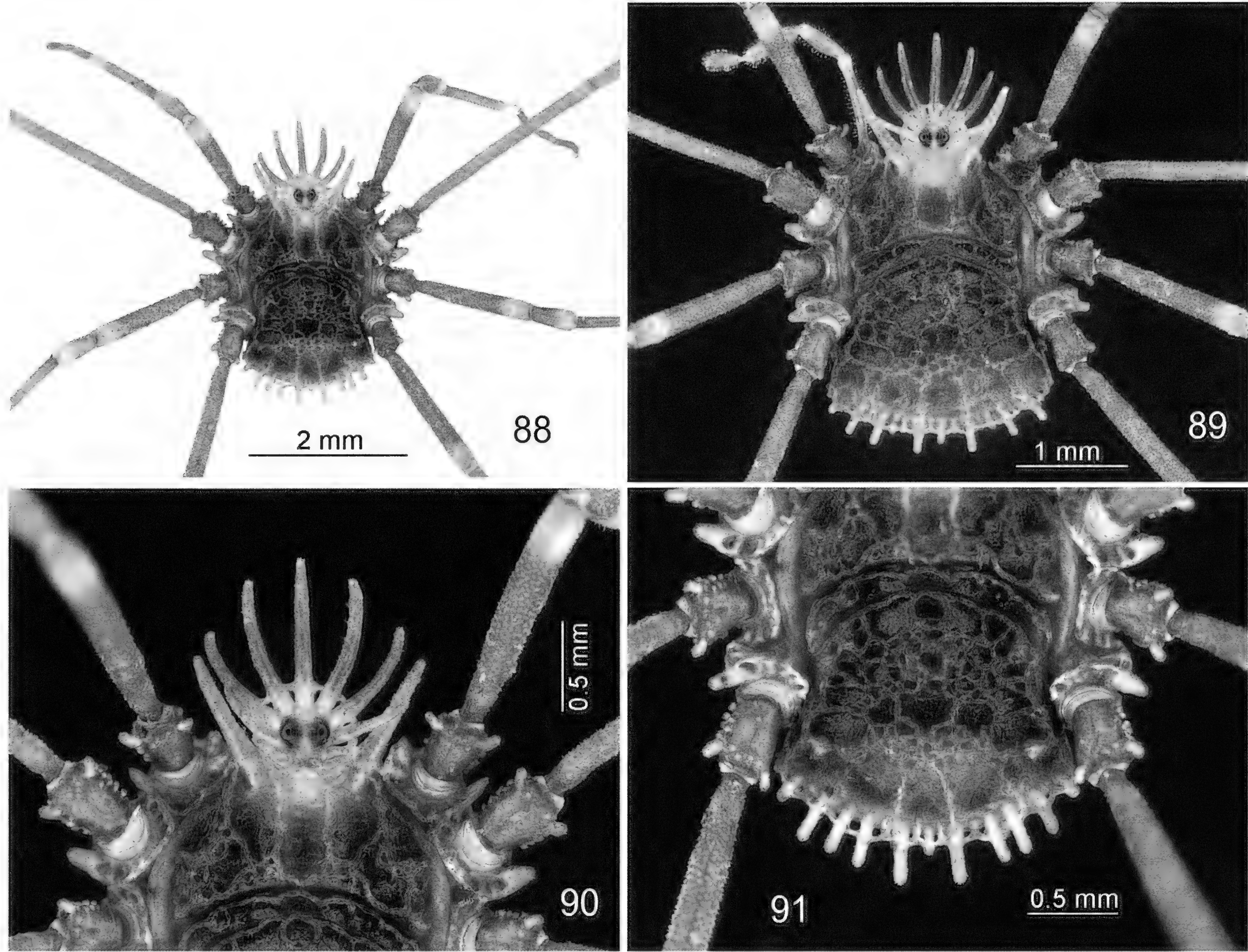
Posterior margin of opisthosoma with a row of eight long tubercles of various lengths, parallel-sided and slightly rounded at tips, longest ones in mid-part of row; tubercles close to basis interconnected by bridges of short lateral-basal denticles resulting in small "windows" (Figs 89, 91); fine texture of microtubercles all round.

Network of prosomal and opisthosomal keel cells made of anvil-shaped tubercles low, forming few large cells in anterior part of prosoma, largest ones behind Tu oc, in parts of metapeltidium no closed cells but an irregular double row of tubercles; on opisthosoma large cells on anterior and posterior margin and on lateral sides, in central part of opisthosoma most cells small except for a large central one, always bounded by low anvil shaped tubercles. All cells blackish in color, slightly lighter keels contrasting with dark smooth cuticle.

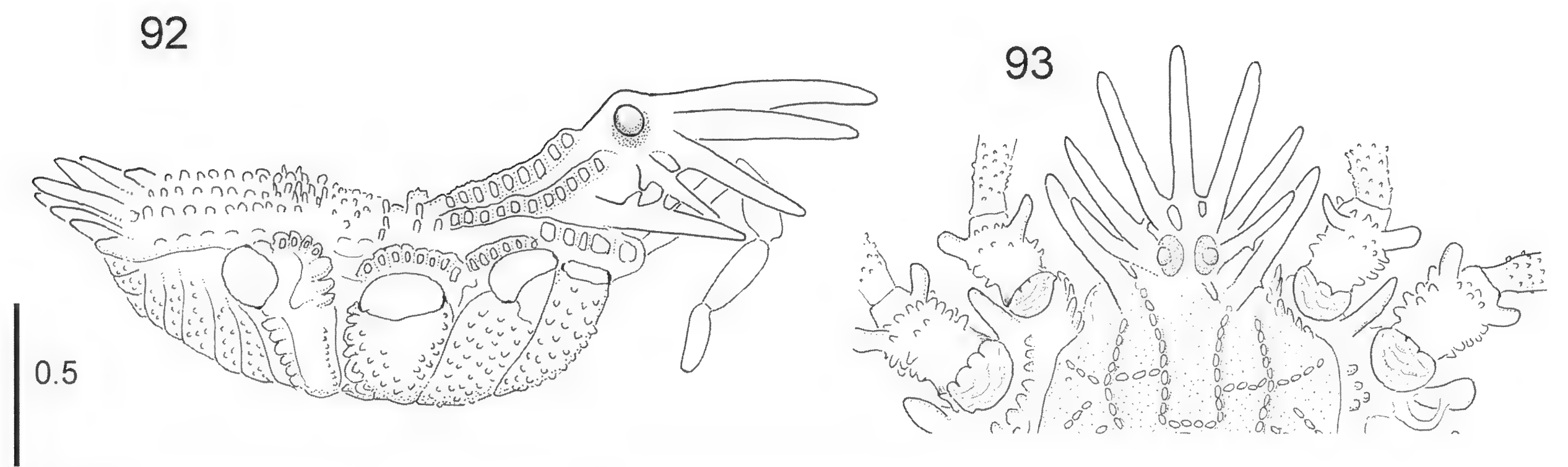
Body, ventral side: Front and back side of all Cx of legs with row of tubercles, on Cx I pro- and retro-la, Cx II retro-la, Cx III pro- and retro-la, Cx IV retro-la; on Cx I tubercles markedly elevated and anvil-shaped, space between rows of tubercles densely covered with minute pointed denticles; free sternites, corona analis and free tergites bent to ve side, covered with low tubercles and fine microtexture, scattered low setae in between.

Tubercles on Tr: I 1 each pro-la and retro-la, II 1 pro-la, 1 retro-la, III 1 pro-la and 1 retro-la, IV 1 pro-la, 1 retro-la.

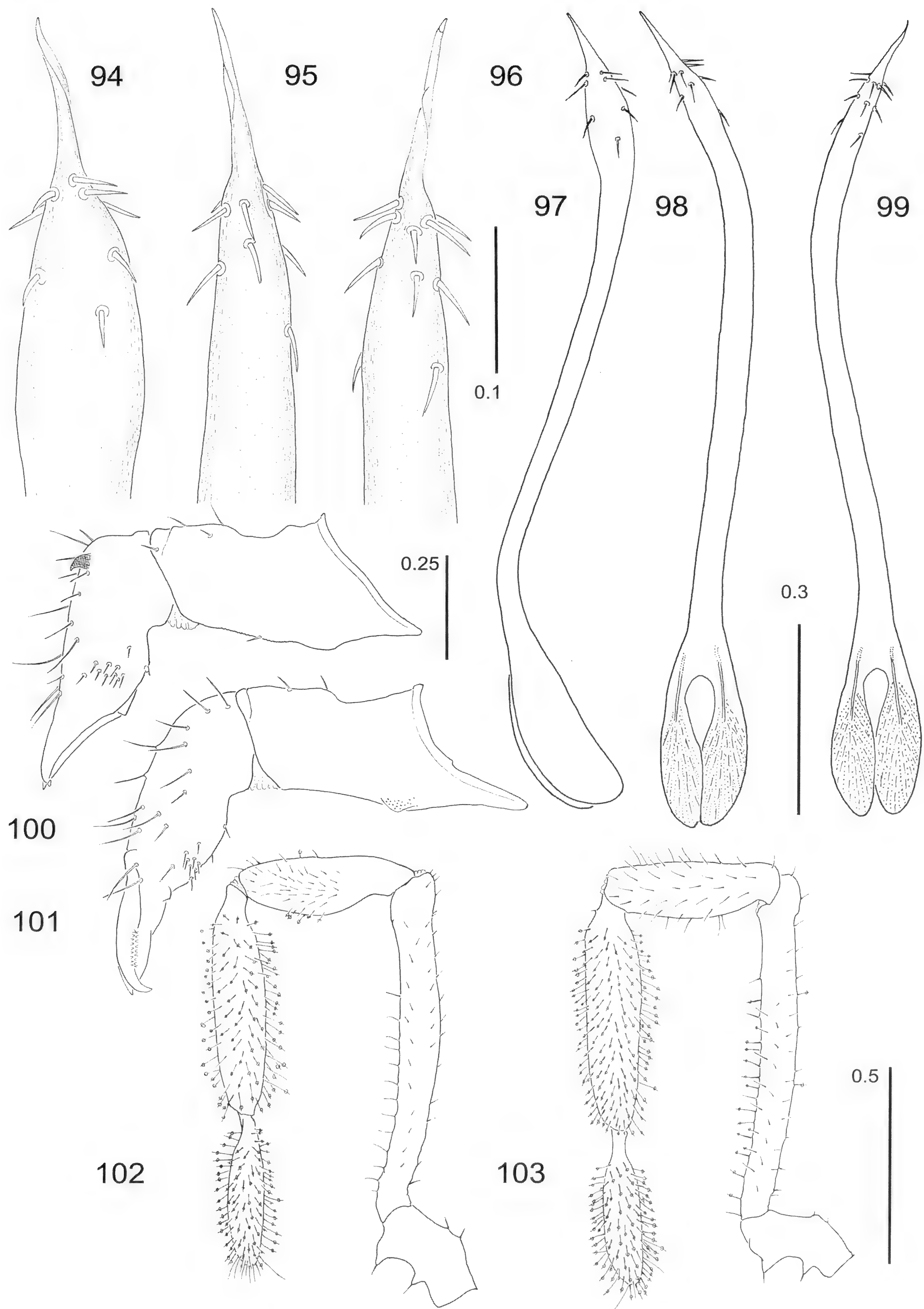
Legs (Figs 88-89, 91): Light brownish, Mt and Ta contrastingly blackish, conspicuously long and slender, no article inflated, covered with densely packed light tubercles and fine setae; long apically rounded tubercles on Cx: I retro-la, II 1 retro-la, III -, IV 1 pro-la, 1 retro-la; articles of Ta (male, female in parenthesis; hyphen separating numbers of different individuals, forward slash indicating difference between right and left side of one individual): leg I 5 (5/4), II 5-6 (4/6), III 6 (7), IV 7 (7).



Figs 88-91. *Asiolasma schwendingeri* sp. nov., dorsal view of male paratype (88, 90-91) and of female paratype (89). (88-89) Entire body. (90) Prosoma. (91) Opisthosoma. Photographs by J. Schmidt.



Figs 92-93. *Asiolasma schwendingeri* sp. nov., male holotype. (92) Entire body in lateral view. (93) Prosoma in dorsal view. Scale: 0.5 mm (92-93).



Figs 94-103. *Asiolasma schwendingeri* sp. nov., male holotype (94-100, 102), female paratype (101, 103). (94) Glans penis in lateral view. (95) Same in ventral view. (96) Same in dorsal view. (97) Whole penis in lateral view. (98) Same in ventral view. (99) Same in dorsal view. (100-101) Right chelicera in prolateral view. (102-103) Right pedipalp in prolateral view. Scales: 0.1 mm (94-96); 0.3 mm (100-101); 0.25 mm (97-99); 0.5 mm (102-103).

Chelicera (Fig. 100): Basal article slightly tapering distally (la view), dorsally slightly constricted, set with few setae dorsally and prolaterally, no brush of setae, no obvious glandular tissue. Second article with a strong apophysis on upper front, pointed, bent downward. Short to long setae on various parts, mainly on 2nd article.

Pedipalp (Fig. 102): Tr slender, slightly swollen on do side, with two marked tubercles on ve side, each pointed and carrying a strong seta; Fe extremely long and slender, slightly curved downwards, slightly enlarged distally and inflated near insertion of Pt, set with few scattered normal hairs; Pt slightly enlarged and bulge-like ventrally, with a loose field of short setae prolaterally, few clavate setae ventrally, no apparent glandular tissue below; Ti cylindrical and slender, with basal stalk, not curved, clavate hairs on all sides; Ta more slender than Ti, stalked, not inflated on do side, densely covered with clavate setae all round, few long and thin hairs at apex.

Genital morphology (Figs 94-99): Penis very long and slender, about two-thirds of body length, slightly curved, basis slightly broadened, deeply split into two parts, two muscles concentrated there; truncus slender, slightly compressed, parallel-sided (ve/do view), slightly broadened from base (la view) towards glans and further towards stylus (do/ve view), glans spindle-shaped and broadened (la view), stylus short and in strait continuation of glans, with slight helical torsion. Armature of glans with uniformly long spindle-shaped spicules arranged in three groups from distal to proximal: i) six in somewhat irregular annular arrangement, symmetrical on do and ve side, ii) four spicules arranged in a ring, one each on do, ve and la sides, iii) two spicules distinctly separated from group ii, one on each la side.

FEMALE (Fig. 90): Similar to male in general appearance of body, anterior hood and opisthosomal tubercles. Chelicera (Fig. 101) without pointed tubercles on 2nd article; pedipalpal Fe (Fig. 103) with scattered clavate setae ventrally but not in distal quarter; Pt less enlarged than in male, other articles as in male. Tubercles at posterior end of opisthosoma (Fig. 89) shorter than in male and slightly thicker.

Measurements: Body length of individual males: 3.4, 3.4, 3.6 (n=3), of females: 3.7, 3.7 (n=2). Leg II: male, female in parentheses: Fe 3.4 (3.1), Pt 1.0 (0.9), Ti 2.9 (2.9), Mt 1.8. (1.7), Ta 2.0 (1.3). Penis length: 1.3.

Variation: Somatic morphology quite homogeneous, but slight variation in lattice keel network of do side of prosoma discernible.

Relationships: Most similar and geographically closest is *A. damingshan* from the southern Chinese province of Guangxi. *Asiolasma schwendingeri* sp. nov. and *A. damingshan* clearly differ in body size, form of anterior hood, proportions and size of male and female pedipalp, pattern of do keel cells and genital morphology, especially armature of glans penis.

Distribution (Fig. 1): Until now this species is known only from a sole locality in Vietnam, Mt Ba Vi, Ba Vi District, Ha Noi Province. The specimens examined were collected in an evergreen forest between 900 m and 1070 m. Adults as well as small juveniles were found in mid May at the beginning of the southwest monsoon when collecting activity is not yet hindered by heavy rainfall. The distance to the type locality of *A. damingshan* in Guangxi Province, China, is approximately 425 km in northeast direction.

Asiolasma billsheari sp. nov.

Figs 1, 104-117

Holotype: SMF; male; CHINA, Gansu Province, western part of Qinling Mountains, 125 km northwest of Longnan, southern side of Lazikou pass, Zhuli valley, 2260 m, 34°07'57"N, 103°56'15"E, north slope, mixed oak/pine forest near creek, moss and litter sifted; D.W. Wrase leg.; 3.8.2012.

Paratype: CJM 8146; 1 male; collected together with holotype.

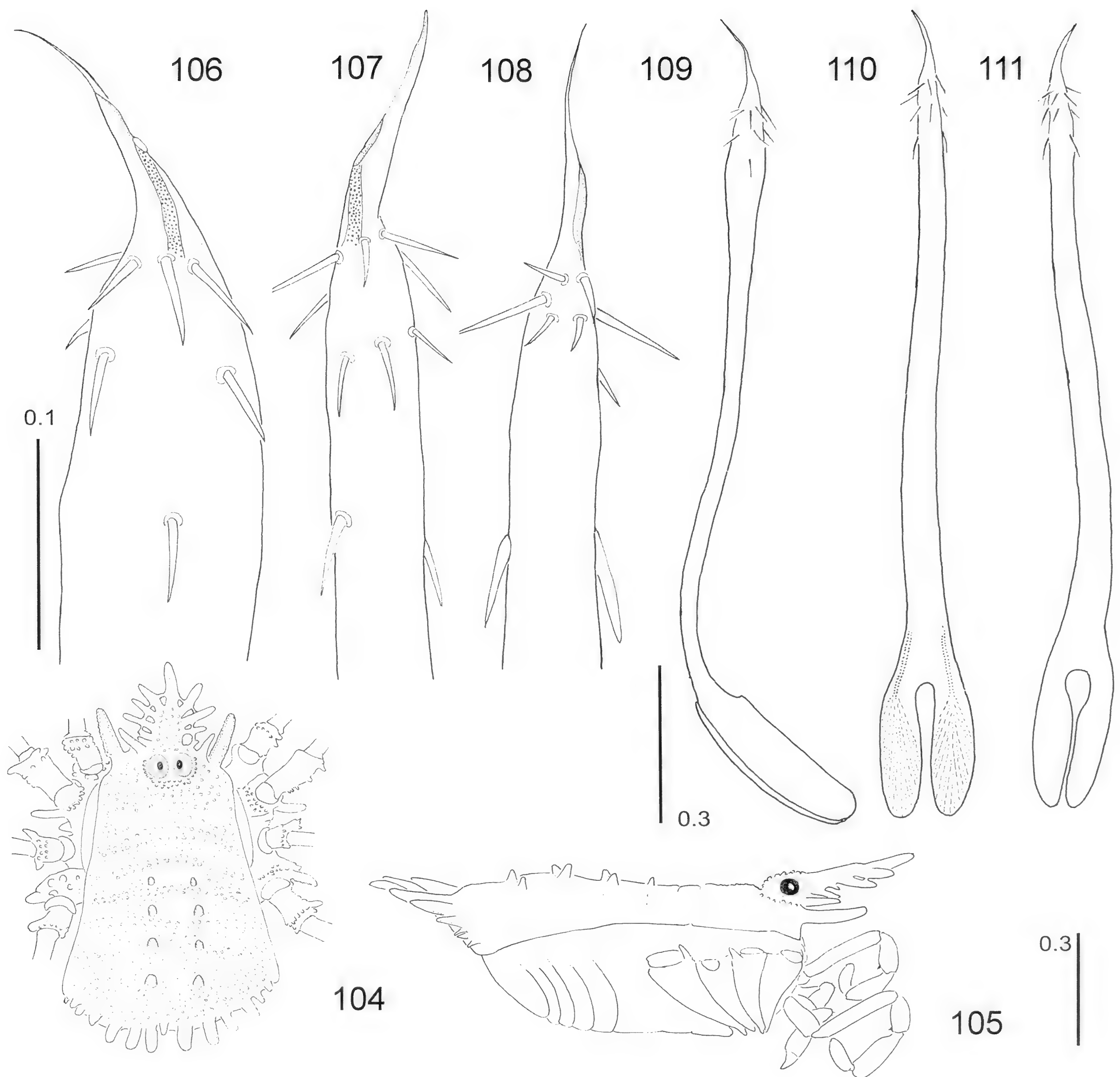
Diagnosis: A relatively small species with rather flat body and short hood; only prolonged anterior part of prosoma with eye mound and hood slightly elevated, similar to geographically close species *A. juergengruberi* sp. nov. from northern Yunnan; body less massive than in *A. schwendingeri* sp. nov. from northern Vietnam, caused by smaller hood processes. Pt of pedipalp with a bent and pointed medio-distal apophysis; areae I-IV of opisthosoma with one paramedian pair of low tubercles.

Name: The species is dedicated to William A. Shear, an esteemed arachnologist and myriapodologist who, together with Jürgen Gruber, meticulously studied New World ortholasmatine harvestmen. Name in genitive case.

Description

MALE

Body, dorsal side (Fig. 104-105): Body rather flat but less so than in *A. schwendingeri* sp. nov. (la view); Tu oc on anterior margin of prosoma only slightly elevated, with a rather low ascent and only slightly elevating eyes; these close to anterior margin of prosoma and hardly integrated into proximal portion of hood, central hood tubercle slightly bent upwards (la view); hood bearing one central unpaired and four or five (unequal on left and right side) lateral paired tubercles, basic one shortest (less than half size of next one or nearly equal size of following one; number of tubercles different on left and right side of hood; Fig. 104), the following ones consecutively longer, last one shorter than central unpaired one; all tubercles interconnected by small anvil-shaped bridges close to their bases; on both sides of hood one short and one long



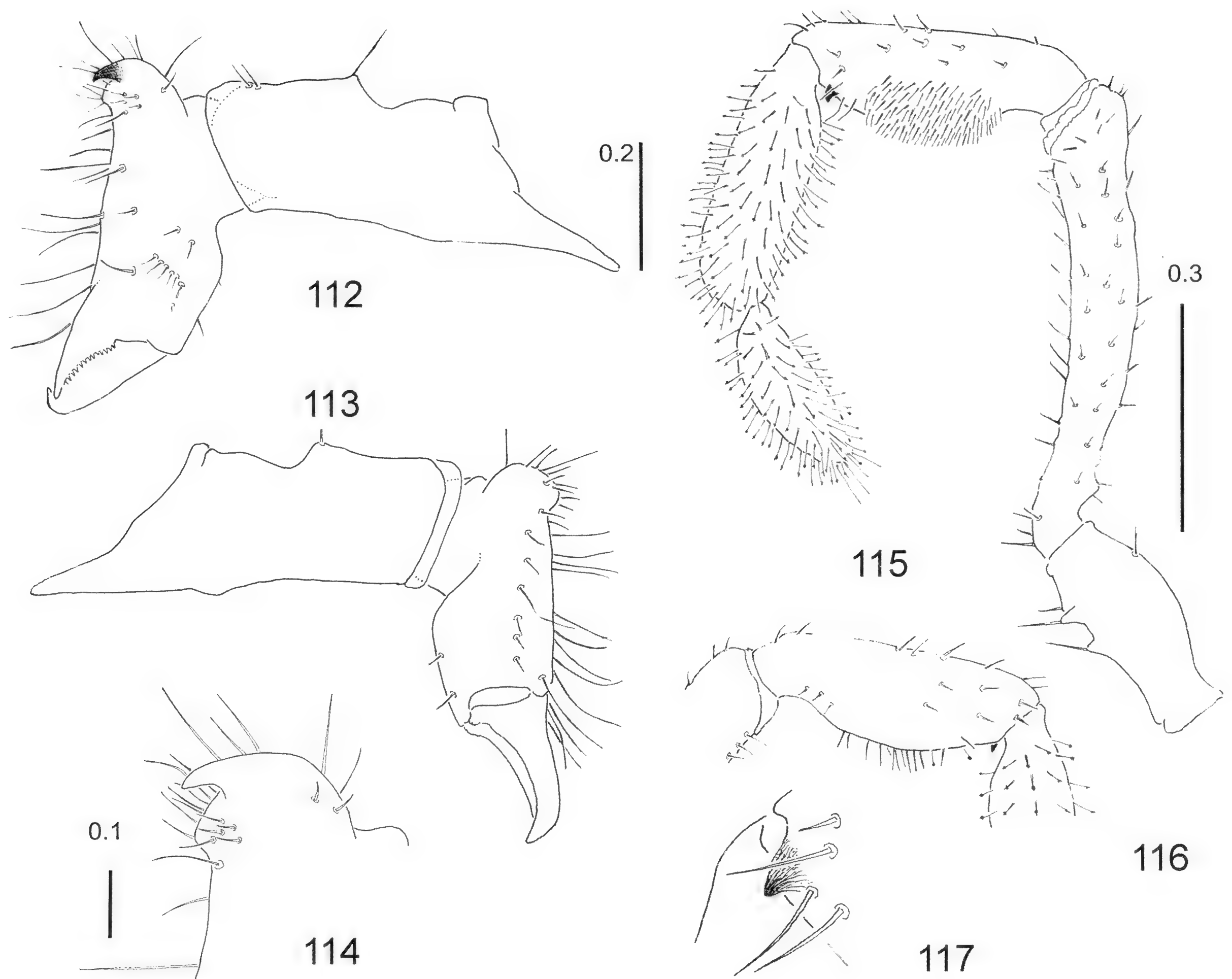
Figs 104-111. *Asiolasma billsheari* sp. nov., male holotype (104, 106-111), male paratype (105). (104) Entire body dorsal view. (105) Same lateral view. (106) Glans penis in lateral view. (107) Same in ventral view. (108) Same in dorsal view. (109) Truncus penis in lateral view. (110) Same in dorsal view. (111) Same in ventral view. In Figs 106-108 subdistal opening of sperm duct is indicated, end of sperm duct is filled with sperm. In Fig. 105 armament with low tubercles on do and ve side of body not shown. Scales: 0.1 mm (106-108); 0.3 mm (104-105, 109-111).

apophysis projecting from anterior margin of prosoma and closely flanking hood, these apophyses thick and massive, covered by small warts. Posterior margin of opisthosoma with a row of 14 tubercles of different lengths, slightly tapering towards markedly rounded tips, longest tubercles in centre and in right part of row. Areae I-IV of opisthosoma with one para-median pair of low indistinct pegs, distal pair shortest, all others of about equal size (do/la view).

Network of keel cells indistinct, only few closed ones on prosoma laterally; on prosoma scattered anvil-shaped

tubercles also in curved transverse rows; on metapeltidium one transverse row of tubercles; on opisthosoma keel cells nearly lacking, no closed cells except for few small ones near lateral margins and additional smaller ones on area V of scute near posterior margin, these cells not always closed; 1-2 transverse rows of anvil-shaped tubercles on areae I-IV of scute partly interrupted.

Body, ventral side: Cx with longitudinal rows of low light tubercles, similar tubercles on Op gen, free sternites and corona analis; free tergites bent to ve side, with transverse rows of tubercles as well.



Figs 112-117. *Asiolasma billsheari* sp. nov., male holotype. (112) Right chelicera in prolateral view. (113) Same in retrolateral view. (114) Apophysis of 2nd cheliceral article in prolateral view. (115) Pedipalp in prolateral view. (116) Distal part of pedipalpal femur, whole patella and proximal part of tibia in retrolateral view. (117) Apophysis on ventro-distal part of pedipalpal patella in prolateral view. Scales: 0.1 mm (114); 0.2 mm (112-113); 0.3 mm (115-116); no scale (117).

Legs: Short, brownish, without darker marks; Fe I and F II slightly swollen, Fe II with slight shallow constrictions; fine microtexture on all articles except Mt and Ta, the latter with fine setae. Tarsal articles of legs I-IV of holotype, of male paratype in parenthesis; in Ta I different numbers on right and left side: I 6 (5/6), II 9 (9), III 6 (6), IV 6 (6).

Chelicera (Figs 112-114): Posterior part of basal article markedly invaginated dorsally (la view), set with one long elevated seta dorsally and few small setae dorso-distally; 2nd article with a strong massive apophysis on upper side, ending in a pointed hook, bent in anterior direction; rounded rather flat apophysis-like edge below hook (la view). Setae of various sizes situated on hook, otherwise mainly on frontal and prolateral sides of article. Only broad apophysis, not pointed hook visible in la view: no brush of setae present and no obvious glandular tissue.

Pedipalp (Figs 115-117): Tr slender, slightly swollen on do side; two small tubercles distally on ve side, each

pointed and carrying a strong seta; Fe long and slender, slightly bent downwards, slightly enlarged distally, set with few scattered normal hairs, no clavate hairs; Pt markedly enlarged and bulge-like ventrally except for basal part, ventrally and partly prolaterally with a dense field of short setae, no apparent glandular tissue below this brush-like field, a small pointed ventro-prolateral hook close to distal margin of article; Ti cylindrical and slender, with indistinct basal stalk, not curved, with loose cover of clavate hairs on all sides; Ta slenderer than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round, distally few long and thin setae interspersed.

Genital morphology (Figs 106-111): Penis very long and slender, more than two-thirds of body length, slightly curved, short basis deeply split into two parts, two muscles concentrated there, penis shaft partly parallel-sided, partly continuously tapering to level of proximal pair of spicules and slightly depressed (ve/la view); penis

(la view) markedly broadened at base and extremely slender above, only slightly enlarged towards glans; glans spindle-shaped and broadened (la view); stylus short and in straight continuation of glans, with slight helical torsion, opening of sperm duct subdistal, sperm in distal end of sperm duct.

Spicules of glans nearly uniform in size and spindle-shaped, arranged in four groups between distal portion of glans and distal part of truncus: i) two spicules on do side, ii) six spicules forming ring on ve, la and do sides, iii) two spicules on each lateral side, iv) one spicule on each lateral side on truncus well below glans armature.

FEMALE: Unknown.

Variation: The armature of the glans is the same in both specimens available. Otherwise no data can be given due to the lack of sufficient material.

Relationships: This species occupies a rather isolated position, but it appears to be closely related to the other species with a massively elevated apophysis of the 2nd cheliceral article, *A. ailaoshan* and *A. juergengruberi* sp. nov. *Asiolasma ailaoshan* is strikingly different in its sexual dimorphism, i.e. the sole known female is much larger than the corresponding male. This dimorphism may also be revealed when the unknown female of *A. billsheari* is discovered. The apophysis of the hood is (absolutely and relatively) shorter in *A. billsheari* sp. nov., thus forming a less broader and less palmate fan cover for pedipalps and chelicerae than in *A. schwendingeri* sp. nov. The minute pegs on the do side of the opisthosoma are absent in *A. ailaoshan* and *A. schwendingeri* sp. nov.

Measurements: Body length (including hood and opisthosomal tubercles) of males: 3.0-3.05 (n=2). Leg II: Tr 0.3, Fe 2.6, Pt 0.8, Ti 2.0, Mt 2.0, Ta 1.6. Pedipalp: Tr 0.3, Fe 0.7, Pt 0.4, Ti 0.45, Ta 0.8. Penis length: 1.7.

Distribution (Fig. 1): The species is only known from the type locality in the Chinese Gansu Province at about 34°N and represents the northernmost known locality of ortholasmatines on mainland Asia (and in Asia in general including the Japanese records of *Cladolasma parvulum*). The two specimens were collected from soil litter in a pine and oak forest at 2260 m altitude.

DISCUSSION

The Nemastomatidae is mainly a Holarctic family of ground-living Dyspnoan harvestmen. According to Shear & Gruber (1983), they are separated into the following two subfamilies: Nemastomatinae Simon, 1872 with a primarily West Palaearctic distribution, and Ortholasmatinae with a strong Nearctic affiliation. While no native nemastomatine species are known from the New World, there are a few ortholasmatines in the Old World, but since first being recorded from southern Japan

(Suzuki, 1963, 1974) species numbers in Asia remained low. Two additional species have recently been discovered in southern China (Zhang & Zhang, 2013; Zhang *et al.*, 2018), and a further three are presented in this paper. This is still a small number despite numerous surveys of the soil fauna in the Himalayas and in Southeast Asia for several decades and, more recently, in China by a number of European and Chinese institutions. Although more species will most likely be discovered in the future, “a wealth of new species to arise from ongoing exploration” of (sub)tropical Asia (Shear & Gruber, 1983; Shear, 2010) is not yet in sight. Consequently, there is a discrepancy between the species-rich ortholasmatine fauna of the Americas with at least 20 species (Shear & Gruber, 1983, 1987; Shear, 2010; Cruz-López, 2017; Cruz-López *et al.*, 2018) and only seven in Asia.

Cruz-López *et al.* (2018) tried to elucidate the phylogenetic relationships within the Ortholasmatinae in a molecular phylogenetic analysis of several of New World and one Asian species, *Cladolasma parvulum*. Their results, based on seven species and one specimen each, are not yet convincing. Their phylogenetic trees establish the only Asian species analyzed as sister to an unidentified *Ortholasma* species (CO1 gene; maximum likelihood) or as sister of *Dendrolasma mirabile* (18S gene; bootstrap). Presently, statistical support for both combinations is low and the molecular phylogenetic relationships of Asian and New World species are still open to question.

Historical biogeography of ortholasmatines: This subject was discussed by Shear & Gruber (1983) and Shear (2010), albeit without a satisfying conclusion achieved. Shear & Gruber (1983) primarily proposed an origin of the subfamily in Asia, with a later dispersal to America, but Shear & Gruber (1983) and Shear (2010) also discussed an alternative scenario and placed the origin of ortholasmatines in the New World, namely, in the central Mexican highlands, or Transverse Volcanic belt, with subsequent dispersal to the northern parts of America, especially to the western coastal areas and southwards to the southern parts of México and even Honduras. Only subsequently did the ortholasmatines enter East Asia. In the light of newly available material the latter scenario is neither very plausible nor convincing and I strongly favour the hypothesis of an Asian origin of the Ortholasmatinae. There are a number of arguments to justify and extend the original hypothesis of Shear & Gruber (1983).

The most prospering group of Nemastomatidae is the nominate subfamily which presently encompasses about 120 species in 18 genera (Schönhofer, 2013). They are confined to the western Palaearctic, with a few outlying species in Central Asia and China (the genera *Starengovia* Snegovaya, 2010 and *Sinostoma* Martens, 2016, comprising three and one presumed relict species, respectively). Regarding the high diversity of Nemastomatidae in western Eurasia, one may assume

that also the ortholasmatines have originated in Asia, not in its montane nor boreal parts, but in its tropical to subtropical parts like present-day southern China and adjacent areas of northern Thailand and northern Vietnam. I further assume that stem ortholasmatines, in accordance with one of the hypotheses of Shear & Gruber (1983), later reached the New World where they underwent a strong radiation into various morphological and ecological lines. This went hand in hand with a considerable geographical range extension from near the Alaskan border, a boreal area, to the Honduran tropics (Shear, 2010). This radiation led to diversification into five genera in the Americas (Shear, 2010; Schönhofer, 2013; Cruz-López *et al.*, 2018).

The Asian ortholasmatine species show a number of plesiomorphic morphological characters, which indicates that they all still live in their ancestral homeland and are not the descendants of American species. My four main reasons for the Old World origin of ortholasmatines are as follows.

1. *Dorsal latticework*: It appears irregular in Asian species, often not arranged into clearly defined cells, and the anvil-shaped tubercles forming the cells are mostly low, sometimes even difficult to recognize (especially so in *Cladolasma parvulum*). I judge this to be a plesiomorphic character state. In the majority of American species there is a regular symmetrical network of keel cells made of interconnected anvil-shaped tubercles with the individual tubercle markedly elevated and forming an astonishingly regular and distinct dorsal sculpture, presumably a derived character state. Anvil-shaped tubercles are exceedingly developed in *Cryptolasma* where they are present also on the dorsal side of the hood. The individual tubercles are fragmented into many minute branches which are spread in various directions.

2. *Male genital morphology*: The penes of Asian ortholasmatines are quite simple and regarded here as plesiomorphic. The muscle-bearing base of the penis is relatively large, occupying about one fifth of the whole penis. The glans bears uniform and relatively large spicules in a regular arrangement of 2-4 chaplets from below the stylus to the distal part of the truncus (some species do not have spicules on the truncus). The stylus is short, slightly twisted, the opening of the sperm duct is subdistal. The Japanese *Cladolasma parvulum* is an exception in displaying a rather complicated armature of the glans, a presumably derived state.

In the American species the penis is more complicated and apparently derived. The muscle-bearing base is smaller and shorter, the truncus relatively longer (about six times as long as base). The armature of the glans is rather elaborate, with different forms of spicules, larger and smaller ones, even some pointing to the tip of the penis (more uniform in *Ortholasma*). The stylus appears to be extended and it is much longer than the glans, its end recurved, the opening of the sperm duct situated at

the end of a recurved stylus but the top of the stylus is spirally twisted in *Dendrolasma*.

3. *Hood of prosoma*: This is a highly derived character that occurs only in few other dyspnoan families (Trogulidae, Dicranolasmatidae), although details differ considerably (Martens, 1976). In Asian and American ortholasmatine genera the hood is clearly different. In the Asian ones the lateral tubercles of the hood project freely for most of their length, only at their bases are they interconnected by small thorns which stabilize the hood. In American species the often long and delicate tubercles are interlinked by similar projecting thorns, but these are situated at the end of the tubercles, thus giving the hood more stability. The resulting fine net-like structure allows for further forward extension of the hood, and this state is found only in American species (for many details see Gruber & Shear, 1983; Shear, 2010). The more complex hood of American ortholasmatines is regarded as apomorphic.

The hood is completely lacking in Mexican *Martensolasma* species, and this character state is probably apomorphic since it is confined to two species only. This genus has been difficult to include in the Ortholasmatinae by using only morphological characters (Cruz-López *et al.*, 2018) and the molecular phylogenetic analysis is not yet unambiguous. Cruz-López *et al.* (2018) point out that also the monophyly of *Trilasma*, as based on its current diagnosis, is questionable and more separate lineages may be involved. An additional species of Mexican ortholasmatine with an unusual morphology awaits formal description and will render American ortholasmatines even more complex than they look at present (Cruz-López *et al.*, 2018).

The morphological richness of somatic characters, as well as male genital features, is quite poorly developed in Asian species. At present only two lineages, represented by *C. parvulum* on one hand and all hitherto known species of *Asiolasma* gen. nov. on the other, can be recognized. This points towards two old evolutionary lineages represented by scattered relicts. In the Americas the diversity (indeed also with regard to the number of known species) is much higher, indicating a more recent radiation and geographic expansion.

4. *Ecological requirements*: They are quite uniform in the Asian species. All live in humid litter or under pieces of dead wood in primeval forests, montane broadleaf forests, coniferous forests and (sub)tropical evergreen forests, with a closed canopy. This is considered a plesiotypic state and corresponds to that of the majority of nemastomatines which all live in moist soil or litter, sometimes even close to running water (*Paranemastoma bicuspidatum* ([C. L. Koch, 1835] in the European Alps; Martens, 1978). Only one species of nemastomatines is known to climb herbs or low bushes, but only in a moist habitat close to the Georgian Black Sea coast (*Paranemastoma superbum* Redikorzev, 1936; see Martens, 2006). Apparently Asian ortholasmatines do

not inhabit degraded forests with an open canopy and a dry sunlit forest floor. In the Americas the ecological spectrum of ortholasmatines is much larger and includes a number of dry habitats, besides moist habitats in tropical rainforest (Shear & Gruber, 1983; Shear, 2010; Cruz-López *et al.*, 2018). This larger ecological plasticity, as compared to that of Asian ortholasmatines, is considered here as being apotypic.

I conclude that ortholasmatines have probably evolved in the Old World, in what is presently the Southeast Asian tropics, and spread only little into the temperate mountains northwards, like the Qinling Range in southern Gansu. Their ancestors could have entered the New World at a presently undefined moment in time and through unknown routes, "...but this points far into the past, certainly previously to the opening of the present Atlantic..." (Shear & Gruber, 1983). There they developed a considerable diversity of morphological traits, resulting in a larger number of species and five presently accepted genera. They enlarged their ecological spectrum to settle also in dry areas and several extant species do no longer require humid soil litter. Ortholasmatines in the area of their origin have remained few, at least as far as currently known. Their morphological diversity, including genitalic traits, is low and on the basis of morphology only two lineages ranking as different genera are presently recognizable. The Asian clades appear to represent relicts even if more species will be discovered in the future. I thus consider the Asian ortholasmatines as the result of an old radiation, and ancestral emigrants led to an extensive, more recent radiation in the Americas.

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Autumn habitat selection of the harvest mouse (*Micromys minutus* Pallas, 1771) in a rural and fragmented landscape

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Abstract: The harvest mouse *Micromys minutus* has, through nest findings, been documented to live in wetlands in tall sedges and grasses in Central Europe. However, there is very little information on the type of habitat this species uses outside of nesting, because this rodent is difficult to capture in ordinary trapping set ups. In France and Switzerland, the harvest mouse populations have decreased strongly in the past two centuries due to the drastic reduction of its favored habitat. The present study used radiotracking to examine a small population in Eastern France living in a fragmented rural landscape. The aim was to learn more about the habitat and vegetation selection of this population during autumn. The results showed that the most favored habitats were in patches of stinging nettles (*Urtica dioica*) and American goldenrod (*Solidago gigantea*) rather than in their supposedly preferred vegetation type, which are tall grass wetlands. The results also presented migrating behavior in three out of the eight monitored individuals, which lead to the discovery of a possible wintering area in an unmown grassy site around a plant dump. These results suggest that disturbed, but unmown areas are important for the harvest mouse as wintering vegetation and should be available in the surrounding of a reproduction site. The results also showed that wetland management must take into account the affinity of this mammal for areas invaded by American goldenrod, in order to prevent the harvest mouse populations from decreasing in those secondary habitats.

Keywords: Harvest mouse - Radiotracking - American goldenrod - Stinging nettle - Habitat fragmentation.

INTRODUCTION

The harvest mouse *Micromys minutus* (Pallas, 1771) is the smallest rodent living in Europe. The ecology of this inconspicuous animal, like its dietary and habitat preferences, is poorly understood, due to the difficulty to trap and observe it in nature. However, a well-known behavior in harvest mice is their ability to build above-ground nests by tearing up the top part of tall grasses into strings, and by weaving them together. These nests are constructed to be used as a shelter and to litter their offspring. Several pioneer articles studying habitat selection of the harvest mouse (Trout, 1978a; Harris, 1979; Dickman, 1986), describe the presence of this species by the means of nest searching, which has the consequence of mostly disclosing the habitat chosen by the mice during the reproductive period. This means that the preferred foraging habitat of the harvest mouse is not necessarily known and might not be the same as the habitat chosen for resting or reproduction.

The conclusions of studies investigating the vegetation type favored by the harvest mice seem to vary depending on regions. For instance, several authors state that this species is mainly connected to wetlands (Trout, 1978a;

Hata, 2011), while others point out its ability to live in a wider range of habitats, including hedgerow, shrubs, dry meadows and disturbed areas (Dickman, 1986; Harris, 1979; Bence *et al.*, 2003; Wijnhoven *et al.*, 2005). However, this rodent is usually not associated with woody areas, stinging nettles, and wastelands (Wijnhoven *et al.*, 2005).

In Central Europe, the harvest mouse is mostly known from marshes and wetlands dominated by tall grasses (*Molinion*, *Phragmition*), or tall sedges (*Caricion*) (Rahm, 1995; Haberl & Kryštufek, 2003; Surmacki *et al.*, 2005; Blant *et al.*, 2012). Unfortunately, these types of vegetation have substantially decreased in France and Switzerland during the past two centuries (Brinson & Malvárez, 2002; Gimmi *et al.*, 2011). Fragmentation and habitat loss have a significant negative influence on wetland species in general (Nilsson & Grelsson, 1995; Lienert *et al.*, 2002). Furthermore, expansion of invasive species like the Japanese knotweed *Reynoutria japonica* (= *Fallopia japonica*) (Polygonaceae) or American goldenrods [*Solidago gigantea* and *Solidago canadensis* (Asteraceae)] also affects negatively those types of habitats (Nilsson & Grelsson, 1995; SSC, 2000; Zedler & Kercher, 2004).

The main goal of the present study was to increase our knowledge regarding the ecology and behavior of the harvest mouse, in particular its habitat selection in a fragmented environment during the autumn period. This study focused on the vegetation associations selected by the harvest mouse by means of radiotracking. A fragmented tall sedge meadow (*Caricion elatae*) colonized by the exotic and invasive species American goldenrod (*Solidago gigantea*) has therefore been chosen as the study area. In addition to radiotracking, a Capture-Mark-Recapture event was set-up to better understand the overall living conditions of the studied harvest mouse population.

Based on the knowledge gathered on the habitats selected by harvest mice to construct their nests, certain types of vegetation are expected to be favored by this species. In particular, we asked whether:

i) Harvest mice favor the habitat type they are known to prefer during reproduction elsewhere in Central Europe, which are tall sedge (*Caricion*) and/or tall grass (*Phragmition*, *Molinion*).

- ii) Harvest mice avoid patches of stinging nettle and American goldenrod, woody areas and anthropogenic areas.
- iii) Harvest mice stay in the vicinity of the tall sedge meadow where they are captured.

MATERIAL AND METHODS

Study area: The study area was located in France near the village of Greny, in the municipality of Péron (Fig. 1). The size of the study area was 23.1 ha which could be divided into many different types of vegetation types and associations (Table 1, Fig. 2, Appendix 2). The sector where the trapping was set up was a tall sedge meadow (association *Caricetum acutiformis*) of 0.26 ha, growing along a stream named “ruisseau de Chanvière”. This stream was dry during the entire field study period (from mid-August of 2017 to mid-November of 2017). Some smaller patches of the lesser-pond sedge *Carex acutiformis* were also present near the main meadow. Together, the *Caricetum acutiformis* represented around

Table 1. Surfaces of the different habitats present in the study area. The marsh vegetation and grassy areas are the type of vegetation expected to be preferred by harvest mice. Areas invaded by American goldenrods and by stinging nettles had an overall similar surface and availability than the previously mentioned habitat types. Woody areas were the most common type of vegetation in the study area.

Vegetation type	Proportion (%)	Association	Surface (ha)	Proportion (%)
Marsh Vegetation	5.5%	<i>Caricetum acutiformis</i>	0.48	2.06
		<i>Phragmition communis</i>	0.37	1.59
		<i>Mentho-Juncion</i>	0.24	1.06
		<i>Molinion caeruleae</i>	0.18	0.78
		<i>Urtico-Calystegietum</i>	0.36	1.56
		<i>Solidagetum giganteae</i>	1.19	5.14
Dry grassy area	0.54%	<i>Panico-Setarion</i>	0.12	0.54
Woody areas	63.8%	<i>Carpinion betuli</i>	10.69	46.29
		<i>Alnion incanae</i>	0.28	1.21
		<i>Alnenion glutinoso-incanae</i>	3.20	13.85
		Tree plantation	0.56	2.43
Mown areas	15.6%	<i>Molinion</i> (cut down)	0.80	3.47
		<i>Mentho-Juncion</i> (cut down)	1.93	8.36
		<i>Caricetum acutiformis</i> (cut down)	0.08	0.34
		<i>Cynocurion</i> (cut down)	0.79	3.43
Anthropogenic areas	7.89%	Path	0.45	1.96
		Road	1.37	5.93
Total			23.10	100.00

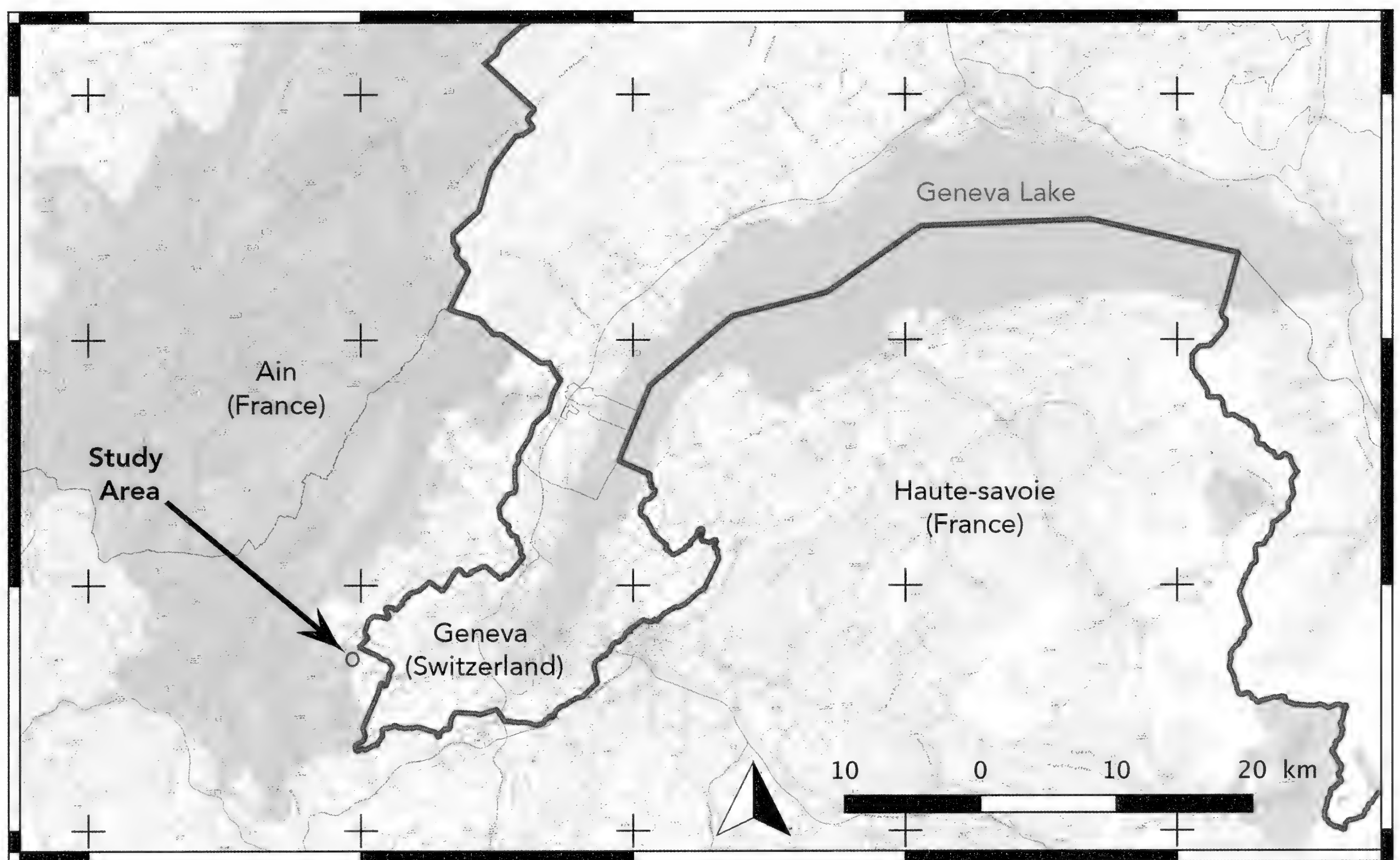


Fig. 1. Map representing the location of the study area. The middle of the main tall sedge meadow is found at the DMS coordinates 46°11'24.4"N 5°57'30.1"E. The study area is situated in the Department Ain, in Eastern France, near the French-Swiss border.

2% of the study area. The area had been shown to be inhabited by harvest mice in 2016, thanks to trapping and the discovery of nests (Gilliéron, 2017).

The habitats surrounding the main meadow included three types of deciduous forests [association *Carpinion betuli* (46.3% of the overall size of the study area), *Alnenion glutinoso-incanae* (13.9%), a tree plantation (2.4%), and an *Alnion incanae* (1.2%)]. In the marshy grasslands (associations *Mentho-Juncion* and *Cynosurion*) adjacent to the main tall sedge meadow, cattle were sometimes present. Some areas were invaded by American goldenrod (*Solidago gigantea*), and by stinging nettles [*Urtica dioica* (L., 1753)], described as characteristic of the alliance *Convolvulion* [associations were respectively *Solidagetum giganteae* (5.1%), and *Urtico-Calystegietum* (1.6%)].

Additional important habitats found in this site were patches of the association *Phragmition* (1.6%) and *Molinion* (0.8%), which are known to be ideal habitats for harvest mice in France and in Switzerland. A plant waste dump was also found near the tall sedge meadow, where a *Panico-Setarion* (0.5%) association thrived. The study area also included a large road constructed in 2001.

Trapping design: A capture-mark-recapture program (CMR) was set up. Trapping was conducted from the second week of August of 2017 to the first week of

September of 2017. A total of 14 trapping nights were completed with 71 INRA traps aligned in 8 transects (Fig. 2, for more details, see below), resulting in 994 trap-nights.

The harvest mouse is a species known for its ability to climb, and has a higher inclination to be captured by traps placed above ground than on the ground (Nordvig, Reddersen & Jensen 2001; Vogel & Gander, 2015). Thus, to increase the probability of capturing the target species over other small mammals, the traps were placed on wooden platforms installed on 60 cm tall sticks (Fig. 3). They were baited with sunflower seeds.

The traps were installed in every substantial patch of tall sedge in and around the main tall sedge meadow. The traps were positioned in 8 line transects and spaced every 1.5 m until reaching the edge of the tall sedge vegetation. Four line transects were placed transversally in the main meadow, with a 10 m gap between each other. In narrower and elongated shaped sedge patches, the line transects were positioned longitudinally.

Initially, it was decided to carry out night-trapping only, with a first check of traps after dusk and a second check after dawn. Because of an overload of wood mice [*Apodemus sylvaticus* (Linnaeus, 1758)] and yellow-necked mice [*Apodemus flavicollis* (Melchior, 1834)], which are both nocturnal rodents, it was decided to

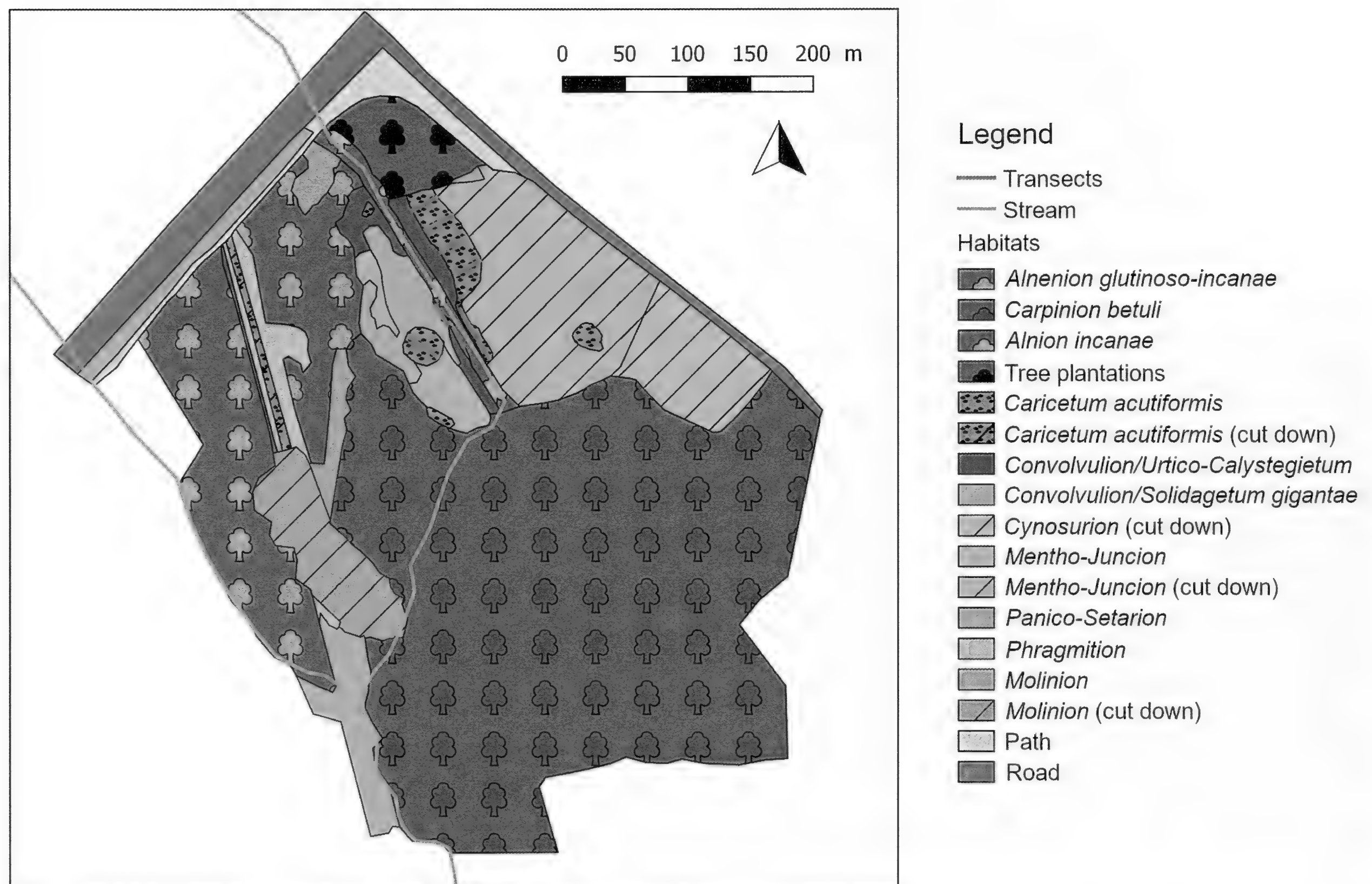


Fig. 2. Map representing the study area and the different habitat types present in it. The *Caricetum acutiformis* patch in the North is the main tall sedge meadow, where most of the study was conducted. The transects (red lines) shown on this map were the ones used for trapping (i.e., for the Capture, Mark and Release event).

activate the traps once during the afternoon for 4 h to capture mice active by day, and once during the evening for 4 h to intercept the nightfall movements.

The trapped harvest mice were marked by means of fur clipping with a small pair of scissors. Their age and sex were documented. The age is very difficult to determine on live harvest mice (Trout, 1978b; Harris, 1979). Therefore, it was decided that individuals weighting less than 6 g and with no apparent primary (testes) or secondary (nipples) reproductive organs were considered as subadults, while the other individuals were considered as adults. The other captured animals were only identified to the species level.

Radiotracking: The tags emitting the position of the tracked mice were glued without anesthesia between the shoulder blades of the captured individuals using veterinary glue. To facilitate the adhesion, the fur was first cut down with a pair of scissors at the implementation area. Among the captured mice, only those weighting at least 5.8 g were selected, for the tag not to exceed 5% of the weight of the equipped animal. The “homing-in” method was applied to locate the tagged animals. It consists of getting as close as possible to the equipped individuals to know their location. The

transmitters chosen for the radiotracking were 0.29 g PicoPip Tags from Biotrack®. These transmitters were relocated with an Australis 26k™ Titley® receiver, which was connected to a Yagi Three Element Antenna (151 MHz) from Titley®. The axis of the antenna was used to indicate the general position of the tag. The receiver was emitting a stronger signal when getting closer to the tags. This material had a maximum detecting range of 50 to 100 m depending on the vegetation density and humidity. The coordinates of the relocations were recorded with a Rugged, handheld Garmin GPSMAP 64®, which approximately had a 3-meter radius error.

The radio-telemetry was performed from mid-September to mid-October 2017. The tagged mice were released at the exact same spot where they had been trapped, defining their first coordinates. All the remaining traps present in the study area were closed to minimize their influence over the mice’s wandering and foraging behavior. The location of the tagged animals was recorded every six hours – if the weather permitted – until the transmitter fell off. The vegetation association was documented on the spot at the same time as the radiotracking and paired with each relocation. The tag could sometimes fall short after the release of the animal or stay put for up to eight



Fig. 3. Set up of the INRA traps, installed in mid-August of 2017 on 60 cm tall sticks, and baited with sunflower seeds. The transect represented here was located in the sedge patch on the South side of the stream la Chanvière. The yellow flowers behind the *Caricion elatae* are the American goldenrod extending nearly to the edge of the forest.

days. Only the individuals that carried the transmitter long enough to be recorded for at least five relocations (which corresponds to at least 24 hours) were kept for the results.

Nest searching and supplementary trapping: A week of trapping was completed from late October to mid-November in the areas where monitored harvest mice were found to spend time (Appendix 1, secondary transects shown as red lines). Nest searching was also carried out in those areas (Appendix 1, shown in grey) to find evidence of long-term occurrence of harvest mice.

Analyses of location data:

CMR (capture-mark-recapture): The size of the harvest mouse population was assumed to be the same as total number of captured and marked individuals during the CMR event.

Radiotracking: The distance between recorded relocations was measured on the QGIS Geographic Information System (Open Source Geospatial Foundation Project)

with the distance matrix analysis. The home range was calculated with RStudio with the package HabitatHR (Calenge, 2015) by combining the GPS coordinates recorded for each tracked individual, using the bandwidth href and including 50% and 80% of the relocations.

RESULTS

CMR: A total of 191 mammals were caught during the first Capture-Marking-Recapture session (Table 2). Despite the high amount of non-target species being caught in the traps by night (188 captures), the harvest mouse was trapped as many times by day (12 times) as by night (12 times). These 24 trapped harvest mice represented 12.6% of the 191 total captures.

Wood mice and yellow-necked mice (*Apodemus* spp.) were the most dominant species during the live-trapping event. They were caught a total of 87 times in eight days, exclusively during the night sessions. The next most dominant species was the bank vole *Myodes glareolus*

Table 2. Results of the CMR event (from the 27th August of 2017 to the 8th of September 2017) in a tall sedge meadow. This represents 8 trappings-nights with 71 above-ground INRA traps. The traps were open 4 hours (day trapping) during the day to capture diurnal activities of harvest mice while avoiding the activity of most other rodents and shrews. The night trapping consisted of 4 hours during the evening to capture nightfall movements.

Species	Day trapping	Night trapping	Total	Proportion
<i>Apodemus spp.</i>	0	87	87	45.5%
<i>Myodes glareolus</i>	6	61	67	35.1%
<i>Micromys minutus</i>	12	12	24	12.6%
<i>Neomys fodiens</i>	2	8	10	5.2%
<i>Sorex minutus</i>	0	3	3	1.6%
Total	22 (10.5%)	188 (89.5%)	191 (100%)	

(Schreber, 1780). Found mostly during the night (61 times), this species was also caught by day (6 times). Two species of shrews were also trapped in the *Caricetum acutiformis*. The water shrew *Neomys fodiens* (Pennant, 1771) was captured 10 times, while the pygmy shrew *Sorex minutus* (Linnaeus, 1766) was captured three times. The 14-day CMR event showed 12 marked individuals (Fig. 4). Those harvest mice were represented by four adult males, three adult females, three subadult males, and two subadults females. All the adult females captured during the CMR event were either pregnant or lactating.

Radiotracking: Eight harvest mice out of the twelve present in the main meadow were heavy enough (5.8 g or above) to carry the transmitter, and kept it for a sufficient amount of time to generate at least five GPS

relocations. The picoPip tags remained on the mice from one to eight days, with a mean of just above three days. The longest distance an individual has moved from its original release point was 350 m.

Wandering behaviors: F1, a pregnant female (12 g, 9 relocations in 54 h), had proportionally the smallest wandering area of all the tracked individuals (Fig. 5, top right). It stayed close to the main tall sedge meadow. Despite this individual being the most closely connected to the *Caricetum acutiformis* of all the tracked mice, only 44% (4 out of 9 points) of the relocations were found in tall sedge. The other relocations were found in the stinging nettle invaded parts of the *Caricion*, (*Urtico-Calystegietum*) and always near American goldenrods.

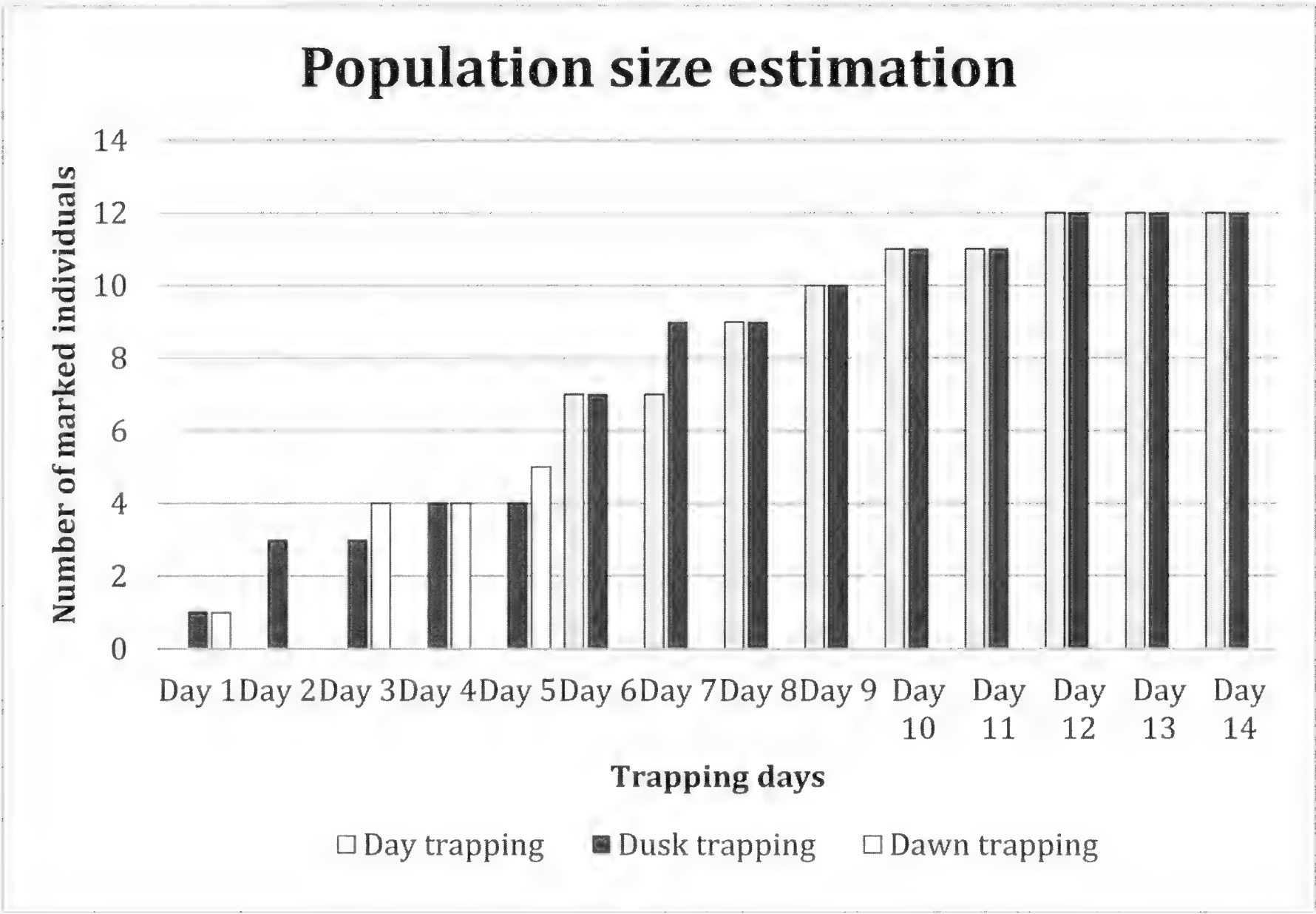


Fig. 4. Accumulated number of marked individuals captured during the CMR event. In the first 5 CMR days, the 71 traps were open 4 h in the evening during the dusk, and 4 hours in the morning during the dawn. The 8 following days (from day 6 to day 14), the traps were open 4 h during the day and 4 h at dusk. The population estimate levelled at 12 individuals, which corresponds to the total number of marked individuals captured during the 14 trapping days.

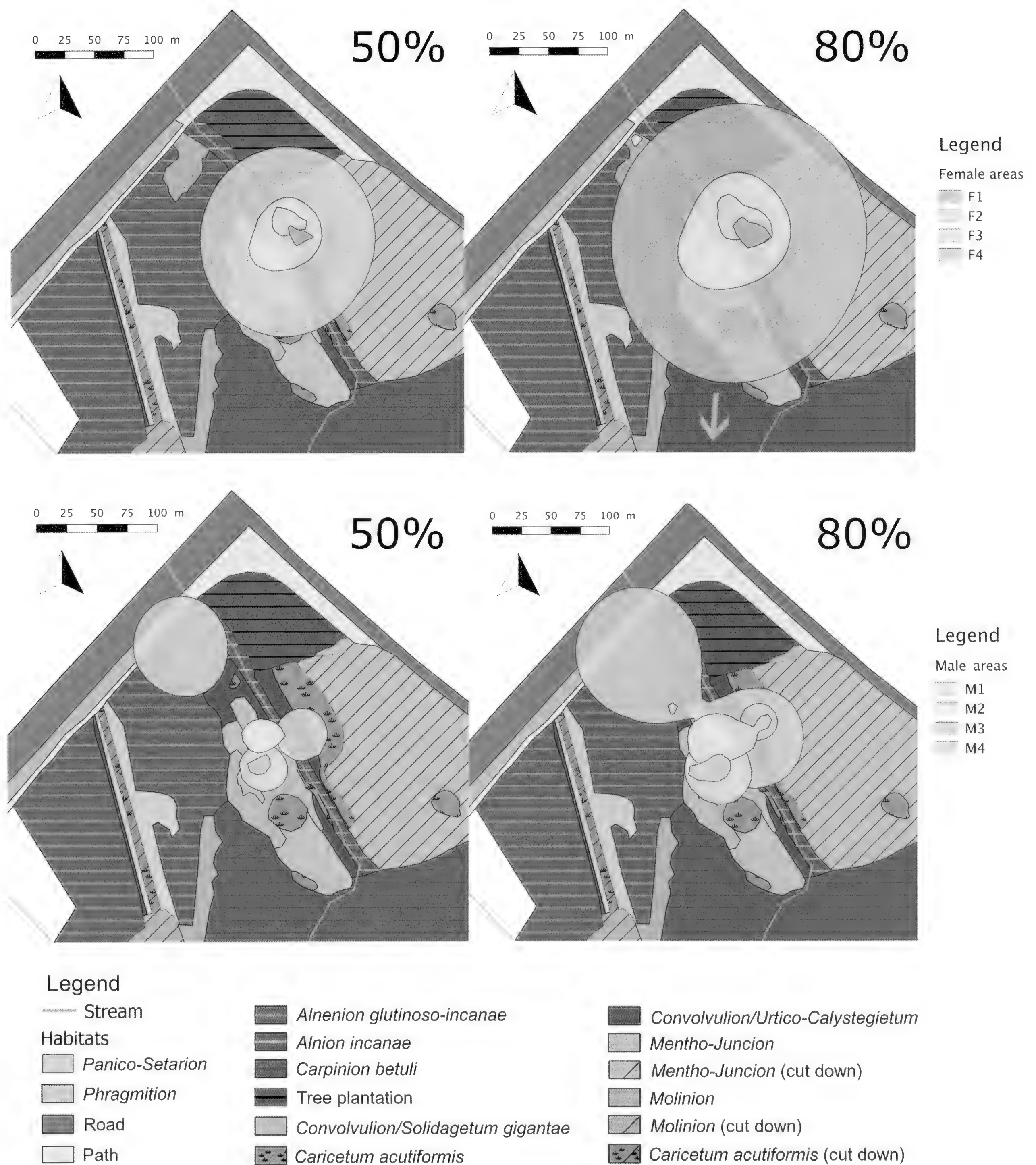


Fig. 5. Wandering areas of the four females (top) and four males (bottom) tracked from mid-September to mid-October of 2017. These ranges were calculated on RStudio with the package HabitatHR. The maps on the left were produced using 50% of the relocations, while the maps on right were produced using 80% of the relocations. These two territory sizes (50% and 80%) help picturing the possible wandering surfaces that may have been used by the tracked individuals. Their actual home ranges were probably between these two representations. Note that female F4 had an additional wandering area outside the presented map (indicated by the arrow on the bottom of the top-right image), when 80% of the relocations were included.

F2, a subadult non-reproductive female (5.8 g, 7 relocations in 40 h), was found equally in tall sedge vegetation and in nettle-invaded areas (43% for each of the habitats). American goldenrods were also consistently present in all the relocations, while not being the dominant plant species.

F3, a non-reproductive adult female (6.1 g, 12 relocations in 96 hours) was relocated near a plant dump, at around 130 meters away from its release point (Fig. 6, bottom left). F3 was located once out of 12 relocations in the *Panico-setarion* which corresponds to the main vegetation found around of the plant dump. It was its last relocation before losing its transmitter. Before moving to the disturbed area, F3 was found 50% in stinging nettles, 25% in goldenrods, and 17% in tall sedge.

F4, a subadult female (5.8 g, 26 relocations in 196 hours) moved the furthest from its releasing point of all the tagged mice (Fig. 6, bottom right). The tag of this female also stayed the longest on its back (eight days). This individual left the tall sedge area, and was found 355 m from its release point, in American goldenrods further south (Fig. 6, bottom right). The radiotracking yielded the same number of relocations in stinging nettles and in goldenrods (46% each), meaning that 92% of the relocations were found in the *Convolvulion* alliance.

M1, a sexually mature male (7.8 g, 5 relocations in 30 h), was mainly found in goldenrods (Fig. 7, top left).

M2, a non-reproductive male (6 g, 14 relocations in 9 hours) also favored the goldenrod habitat *Solidagetum giganteae* with 79% of its relocations (Fig. 7, top right).

M3, a sexually mature adult male (6.8 g, 16 relocations in 97 hours) was relocated in the same a disturbed area as F3 (Fig. 6, bottom left and Fig. 7, bottom left). M3 had 15% of its relocations in stinging nettles, including once in the plant dump area. It was never found in goldenrods. This individual had 56% of its relocations in the *Panico-Setarion*.

M4, a sexually mature adult male (7.8 g, 5 relocations in 26 h) was mainly found in the same area and habitat as M1 and M2 (Fig. 5, bottom).

Habitat selection: A total of 94 GPS points were recorded during the radiotracking survey of the eight harvest mice mentioned in the previous section.

The vegetation type noted simultaneously with the relocations (Table 3) showed that 70% of the relocations were found in the plant alliance *Convolvulion*. This habitat either consisted of the association *Solidagetum giganteae* (American goldenrod patches, 36% of the relocations), or *Urtico-Calystegietum* (mostly represented by sedge patches invaded and dominated by stinging nettles, 34% of the relocations).

The next-preferred habitat used by the tagged harvest mice was the tall sedge meadow *Caricetum acutiformis* (16% of the relocations). It is important to acknowledge that about half of the points (7 relocations out of 15) representing this habitat corresponded to the trapping (and releasing) points of the tracked individuals. Two individuals out of eight moved from the tall sedge meadow to a grassy area with a *Panico-Setarion* thriving around a plant dump, which represents 10.6% of the overall relocations. Finally, three GPS relocations were found in the habitat *Mentho-Juncion*.

Nest searching and supplementary trapping: The nest searches revealed the establishment of harvest mice around the plant dump (*Panico-Setarion*), with a total of 7 green (i.e. fresh) nests found in an area of 1237 m². Yet, no harvest mouse was captured in that area in November during the secondary trapping session, even after eight trapping-nights.

No nest was found in the American goldenrods but a few individuals, including a pregnant female, were caught in the goldenrod patches near the tall sedge meadow, on the South-Western side of the stream. Furthermore, a small tall sedge patch was found on the same side, were at least three nests were found, and a juvenile harvest mouse was trapped.

One old nest (presumably from the year prior the study) was found in reeds (*Phragmition*), but no harvest mice were captured in the transects placed in this habitat.

DISCUSSION

The number of individuals estimated to be alive during the CMR event (12 individuals), showed that very few harvest mice live in the main meadow. This means that the majority of the mice alive (8 out of 12) were

Table 3. Summary of the vegetation associations found in relation to the 94 GPS relocations of the eight harvest mice tracked in October 2017. The *Solidagetum giganteae* association, representing American goldenrod patches, and the *Urtico-Calystegietum* association, representing stinging nettles-invaded sedge patches, were the most favored habitats. The *Caricetum acutiformis* association, which was expected to be the most preferred habitat, represented only 15.9%.

Alliance	Association	Number of relocations	Proportion
<i>Convolvulion</i>	<i>Solidagetum giganteae</i>	34	36.2%
<i>Convolvulion</i>	<i>Urtico-Calystegietum</i>	32	34.0%
<i>Magnocaricion elatae</i>	<i>Caricetum acutiformis</i>	15	15.9%
<i>Panico-Setarion</i>	—	10	10.7%
<i>Mentho-Juncion</i>	—	3	3.2%

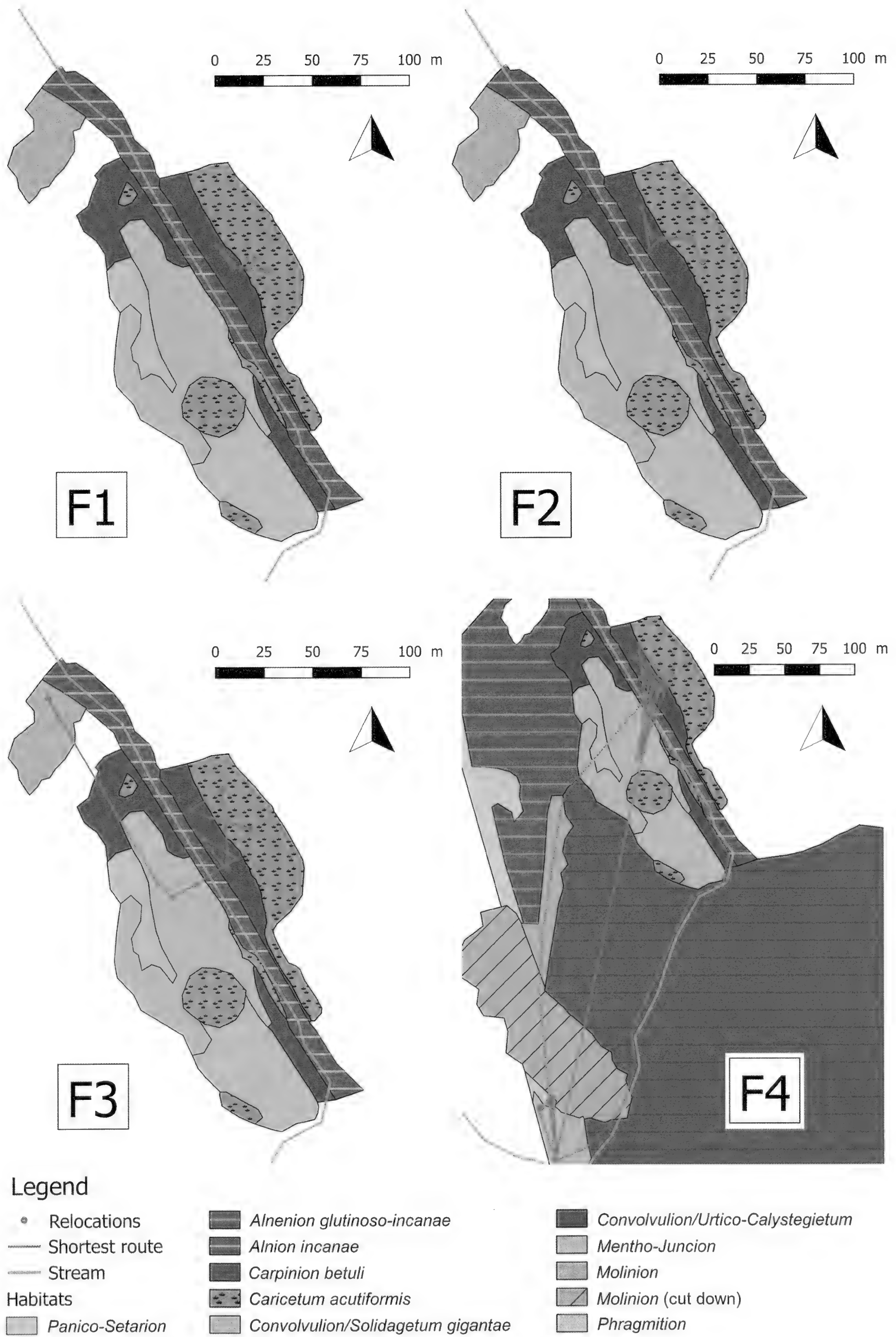


Fig. 6. Relocations of the four female individuals F1, F2, F3 and F4. F1 was tracked from the 17th to the 19th of September 2017. F2 was tracked from the 19th to the 21th of September 2017. F3 was tracked from the 24th to the 29th of September 2017. F4 was tracked from the 29th of September to the 2nd of October 2017. The dashed red line (F4) represents a possible migration route for the female F4.

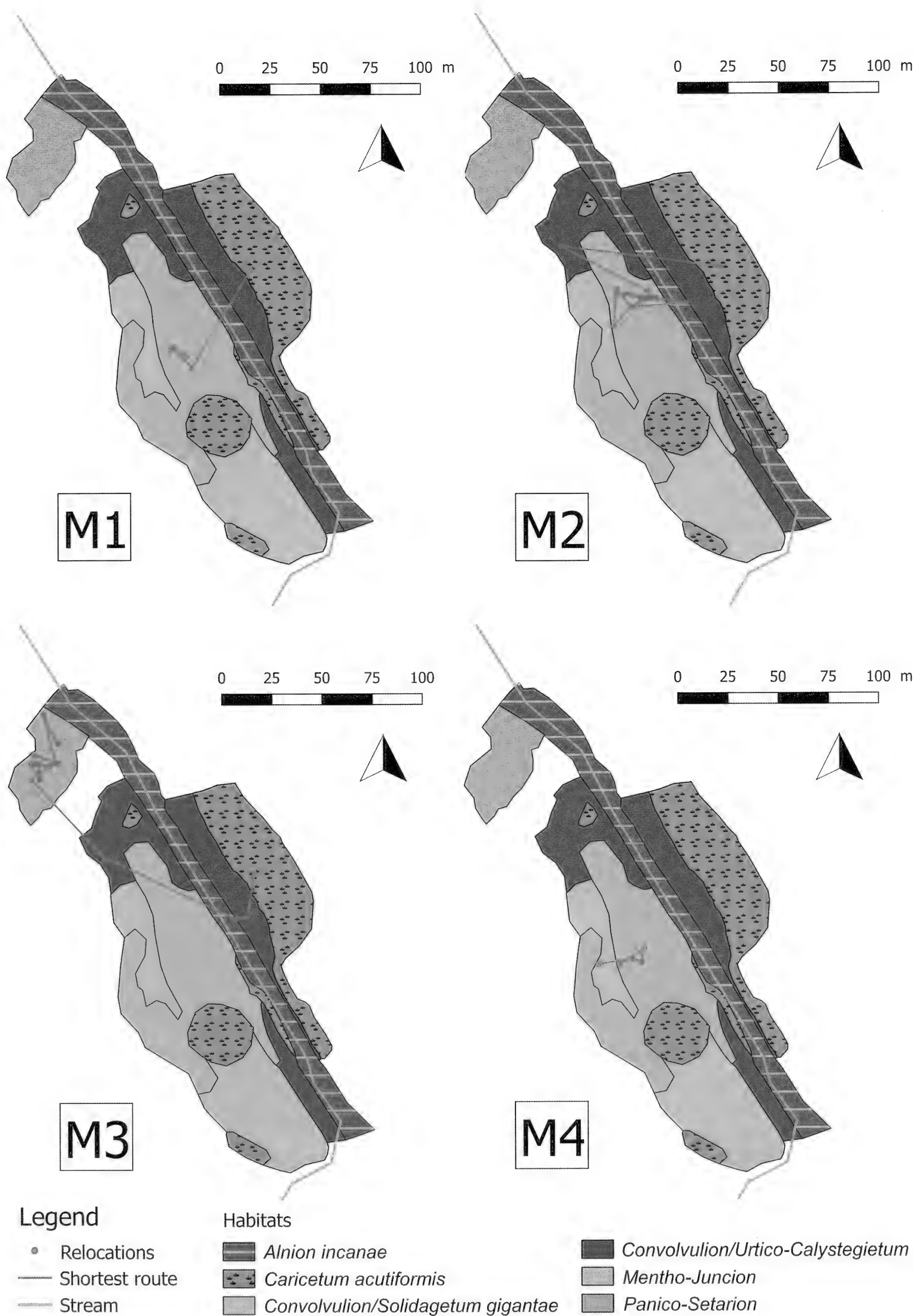


Fig. 7. Relocations of the four male individuals M1, M2, M3 and M4. M1 was tracked from the 19th to the 21th of September 2017. M2 was tracked from the 06th to the 10th of October 2017. M3 was tracked from the 15th to the 19th of October 2017. M4 was tracked from the 15th to the 17th of October 2017.

monitored during the radio-telemetry session. Because of the limited time during which these individuals were tracked (between two and eight days), the results only showed a glimpse of the habitat choices of the harvest mice in this area. Nevertheless, this can be assumed to be representative of the overall behavior of the harvest mice during this period of time.

Movements and habitat preference: The radiotracking revealed unexpected wandering behavior. The hypothesis that the tagged mice would stay within the main tall sedge meadow could be rejected. Indeed, three individuals out of eight showed a migration behavior, and three clearly preferred to stay in the goldenrods on the other side of the stream instead of inside of the *Caricion elatae*. Two individuals out of eight stayed near the main tall sedge meadow, but the majority of their relocations were not found in the lesser-pond sedge.

The calculated ranges (Fig. 5) show that the tracked harvest mice may have overlaying wandering areas according to their sex. Harvest mice tend to have overlapping ranges, but can have aggressive and territorial behaviors during the breeding season (Corbet & Harris, 1991). Aggression is usually characterized by tail biting, sometimes leading to partial tail loss, and this was observed in the two reproductive males, M1 and M4 that clearly had overlaying territories. This could indicate that the goldenrod habitat might be worth defending for male harvest mice.

Corbet & Harris (1991) also noted that harvest mice leave their breeding territory in the winter, and construct smaller, non-breeding nests low in grassy tussocks in their wintering area. Such nests correspond accurately to the nests (at least seven) found in the grasses growing around the plant dump, where two of the tracked individuals (F3 and M3) spent some time. This indicates that this area may very well be a wintering habitat for this population of harvest mice.

F4, the individual that left the main tall sedge meadow to travel more than 350 m in a day, might also have had a similar migration behavior to find a new habitat where to spend the winter. Since this individual was a subadult, this movement may also be explained by the dispersal and exploratory behavior observed on juveniles (Corbet & Harris, 1991).

The path taken by F4 to reach the Southern goldenrod patch is unknown, since the tag was found 25 hours after the previous point, which was located in the main tall sedge meadow. Only assumptions can be made, but two plausible routes might have been taken (see the dashed red lines on Fig. 6). F4 was close to the stream bed when found in the Southern goldenrod patch. This could indicate that F4 followed the stream to find the new habitat. However, harvest mice are not forest dwellers (Wijnhoven *et al.*, 2005). F4 would have had to go through the wooden area *Carpinion betuli* for at

least 200 m, which is not very likely. The second way to reach the Southern goldenrod patch would be to go through the *Carpinion betuli* for 20 m only, on an area where the forest was the narrowest and where signs of other animal movements (Roe deer and fox) were visible. Furthermore, this path leads to a *Molinion*, which is a habitat known to be favored by harvest mice.

Either way, the harvest mouse is not known to be moving or living in wooden areas. Studies capturing a wide number of rodents in several habitats recorded few or no captures of this species in woodland or forests (Canova, 1992; Wijnhoven *et al.*, 2005; Paziewska *et al.*, 2010). Such movements through a forested zone are probably not common for the harvest mouse and is possibly only done during migration to new suitable areas.

After traveling, F4 stayed at least 72 hours in the Southern American goldenrod patch (the transmitter fell off before showing any further migration or wandering behavior), which implies that it was an adequate environment to stay in. This raises questions about why the *Convolvulion* habitat is so interesting for the majority of the tagged individuals. Indeed, all the tracked harvest mice favored this unexpected habitat. They showed a clear preference for stinging nettle and goldenrod invaded habitats (both being part of the *Convolvulion* plant alliance), while neglecting the lesser-pond sedge available nearby. The preference for stinging nettles observed during the radiotracking event is the opposite of what is known about habitat choices of this species in the literature. As a matter of fact, a negative correlation between stinging nettle presence and harvest mouse trapping has been shown (Wijnhoven *et al.*, 2005).

To our knowledge, no author described the relationship between habitats invaded by American goldenrods and the harvest mouse. This study is therefore the first to correlate the wandering behavior of harvest mice with this exotic plant. Several explanations can be hypothesized to explain the inclination of the harvest mice for stinging nettles and for American goldenrods.

The potential importance of stinging nettles: The radiotracking period was set from mid-September to mid-October, which corresponds to the last part of the breeding season for the harvest mouse (Corbet & Harris, 1991). One explanation for the harvest mice to select stinging nettles could therefore be linked to reproduction. Indeed, they might build nests in the stinging nettle-invaded parts, because in the study area, the under layer of the vegetation growing in the *Urtico-Calystegietum* association was mainly lesser-pond sedge. Surmacki *et al.* (2005), and Čanádý (2013) noted the presence of harvest mouse nests in stinging nettles. Yet, both found that this plant is used as nest support in very low frequencies in comparison to other plants, like grasses or hedgerows. Stinging nettles might provide supplementary protection against predation thanks to the very dense layer it formed over the sedge, covering

the aerial view of the invaded part of the meadow. Such affinity of the harvest mouse for dense vegetation cover was already observed by Trout (1978a). Furthermore, the trichomes of the stinging nettles can deter terrestrial predators to search into the vegetation.

Stinging nettles might simply constitute a better foraging habitat and vegetation for the harvest mouse. It has been shown by Dickman (1986) that the small rodent favors seeds, insects, and monocotyledon leaves as primary diet, but also includes dicotyledon leaves and fruits in variable proportions depending on the habitat it lives in. The areas that were largely dominated by lesser-pond sedges might have been neglected due to lower food availability in the form of seeds. Indeed, the monitoring took place in autumn, a period of the year when the sedges had neither flowers, nor seeds. Therefore, based on Dickman's study (1986), it can be hypothesized that this rodent was either interested in seeds or in insects that were present in the nettle invaded habitats.

The potential importance of American goldenrods:

Because of its invasive nature, the American goldenrod was by far the dominant species in the *Solidagetum giganteae* association patches. Almost no other plant was observed growing on the same soil as the goldenrods. The only species that was found near it was the common hop *Humulus lupulus* that was climbing on the flowers of the exotic plant. Nearly no vascular plant was found on the ground. This implies that American goldenrods might have a direct relationship with the habitat preferences of the harvest mouse in the study area. Either the plant itself was interesting to the rodent, or it was a factor directly associated with the exotic species. During the radiotracking period, the American goldenrods were in their seed state. It can therefore be hypothesized that the mice preferred to wander into the *Solidagetum* patch for foraging reasons. They might be interested in the goldenrod seeds, or in insects living in that habitat.

It is unlikely that the harvest mice chose to breed in the goldenrod invaded habitats since there were neither grasses nor sedge growing under the invasive plant. Therefore, nests virtually could not be weaved against them in those areas. The absence of nests found during the nest-searching event supports this hypothesis.

The potential importance of unmown grassy areas:

The third habitat that attracted two harvest mice out of eight was the *Panico-Setarion*. This habitat was located around a plant waste dump mainly colonized with grasses (Poaceae), in particular the barnyard grass *Echinochloa crus-galli*, that was forming dominant patches. This plant species seemed to be very appealing to the two harvest mice relocated in that area, since most of the relocations of the individuals found in this habitat were found in the barnyard grass clumps. This behavior can supposedly be explained by the fact that, at that time, the panicles of this species were full of seeds.

The radiotracking session being performed in October, the lesser-pond sedge was in its vegetative state, meaning that if the harvest mice were searching for seeds, they had to travel to sites involving the presence of unmown grasses. Indeed, this area was the closest place where grasses were fully grown and unmanaged. The *Panico-Setarion* patch seemed to be very attractive for other harvest mice too, since at least 7 fresh nests were found in an area of 1237 m².

Generally, the radiotracking showed the tendency of females to stay closer to the main tall sedge meadow (three females out of four) and stinging nettles, while males (three out of four) tended to stay more in goldenrod invaded areas. The radiotracking data also showed probable winter migration (three individuals out of eight), with a complete change of habitat type for two out of eight individuals, reaching a dry grassy area, rich in seeds.

CONCLUSION

The present study indicates that the breeding sites of the harvest mouse, and therefore habitats where this species' breeding nest are found, might not correspond to its foraging and wintering habitats. This means that trapping and radiotracking procedures are important to add to nest searching when monitoring this species populations and habitat utilization. This is specifically important for wetlands and marshes that are invaded by exotic species and/or suffer from scrub encroachment if not managed regularly and when subjected to eutrophication. Management of site populated by harvest mice must take into account the fact that some unexpected habitats can be used as wintering areas (like the plant dump) or foraging areas (like the American goldenrod and the stinging nettle patches).

The present study showed that the harvest mouse is able to adapt, to some extent, to changes and alterations of its main breeding habitat, like fragmentation, eutrophication, and changes caused by invasion from exotic species, like the American goldenrod, or other nitrophilous species, like the stinging nettles. However, alien species jeopardize the long-term persistence of the tall sedge meadow, which is essential for the mice to weave nests and reproduce. Indeed, alien species have been shown to modify their environment by increasing biomass (Zedler & Kercher, 2004). If no management plan is set up, this increase of biomass may dry up the marshy meadow and create an unsuitable growth habitat for tall sedges. It is therefore important to manage the area in order to keep the tall sedge meadow as it is.

Exotic goldenrods are sometimes fought in a very extensive manner, with complete elimination of the plants, usually combined with the removal of the surface layer of the soil (Canton de Vaud, 2013; AGIN, 2014). This study showed that harvest mice use this type of habitat during autumn, and it is likely that they forage in this vegetation

at other times of the year. Complete removal of the alien species and of the soil in one season are not advised for the study area. Nevertheless, it is highly recommended to keep the American goldenrods out of the main tall sedge meadow to support the population source area. Furthermore, it is advised to contain the spreading of exotic plant by mowing the highly invaded part once or twice a year before the flowering of the plants (Canton de Vaud, 2013; AGIN, 2014).

One should keep in mind that this study followed the tagged mice in a very small portion of the year. This represents only a fragment of the life of the studied individuals, meaning that the same mice might favor other types of vegetation during other periods of the year, depending on temperature, phenology of the plants, phenology of the insects, and their own phenology. Anthropogenic influence of the study area, like periodical mowing and presence of cattle, can also have a considerable impact on the harvest mice's behavior and survival.

Further investigations on the habitat selection of harvest mice in fragmented landscape during other times of the year may bring different knowledge regarding the ecology of this animal. Such information would show when and why the harvest mice have such an affinity for disturbed areas. Further radiotracking events during late autumn may also show what kind of wintering habitats are needed to be preserved to create sustainable vegetation for the harvest mice populations.

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Appendix 1

Secondary transects (red lines) placed in late October to early November of 2017, after the radiotracking event. These transects were set up in areas to which harvest mice appeared to migrate to. Nest-searching was also done (grey areas). The aim was to know if other individuals were present or not in these areas.



Appendix 2

Names and references of plant associations used in this study:

Alnion incanae Pawłowski in Pawłowski, Sokołowski & Wallisch, 1928

Reference: Bardat *et al.* (2004).

Alnenion glutinoso-incanae Oberdorfer, 1953

Reference: Bardat *et al.* (2004).

Carpinion betuli Issler, 1931

Reference: Bardat *et al.* (2004).

Caricetum acutiformis Eggler, 1933

Reference: Devillers *et al.* (1991)

Cynosurion cristati Tüxen, 1947

Reference: Bardat *et al.* (2004).

Mentho longifoliae - *Juncion inflexi* Th. Müll. & Görs ex de Foucault, 2008

Reference: de Foucault & Catteau (2012)

Molinion caeruleae Koch, 1926

Reference: European Topic Centre on Biological Diversity (2008)

Solidagetum giganteae Robbe ex J.-M. Royer *et al.*, 2006

Reference: Bensettiti *et al.* (2002)

Urtico dioicae-Calystegietum sepium Görs & Müller, 1969

Reference: Bensettiti *et al.* (2002)

Panico-Setarion Sissingh in Westhoff *et al.*, 1946

Reference: European Topic Centre on Biological Diversity (2008)

Phragmition communis Koch, 1926

Reference: Bardat *et al.* (2004).

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**A revision of the Chilean Brachyglutini – Part 4. Revision of *Achilia* Reitter, 1890:
A. puncticeps and *A. approximans* species groups, with description of seven new species
 (Coleoptera: Staphylinidae: Pselaphinae)**

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Abstract: The *Achilia approximans* and *A. puncticeps* species groups *sensu* Jeannel (1962) of the species-rich genus *Achilia* Reitter, 1890 are revised. *Achilia puncticeps* (Reitter, 1883) is redescribed, and *A. approximans* (Reitter, 1885) synonymized with it (syn. nov.). Six new species – *A. adorabilis* n. sp., *A. baburra* n. sp., *A. cunniceps* n. sp., *A. nipponobythoides* n. sp., *A. reitteri* n. sp., and *A. trulla* n. sp. – sharing a unique combination of characters with *A. puncticeps* are described, as well as a seventh new species – *A. zaurda* n. sp. – whose male was initially confused with that of *A. puncticeps*. For these species the distribution is detailed, and the habitat/collecting data are summarized.

Keywords: *Achilia* - Chile - taxonomy - new species - distribution.

INTRODUCTION

This article is the fourth contribution to our series aiming at a taxonomic revision of the Brachyglutini of the temperate region of southern South America, and the third that is dedicated to the genus *Achilia* Reitter, 1890 (Kurbatov & Sabella, 2015; Sabella *et al.*, 2017; Kurbatov *et al.*, 2018).

We here focus on the *Achilia approximans* and *A. puncticeps* species groups *sensu* Jeannel (1962). The types of the constitutive members of these two remove informal groups of species – *i.e.* *A. puncticeps* (Reitter, 1883) and *A. approximans* (Reitter, 1885) – are critically reexamined. We present six new species sharing a unique combination of external and aedeagal features with *A. puncticeps*, as well as a seventh new species, whose males have been consistently confused with those of *A. puncticeps* (Reitter, 1885; Jeannel, 1962). Descriptions or redescriptions are given for all of these species, with drawings of their aedeagus and other key characters, as well as images of the male sexually dimorphic heads. Their distributions are detailed, and the collecting data are summarized.

The species groups of *Achilia* as defined by Jeannel (1962), which are mainly based on male sexual dimorphism, as well as their possible phylogenetic relationships will be reassessed later. A key to identification of the species of *Achilia* will be provided only at the end of this series of contributions.

MATERIAL AND METHODS

This study is based on the examination of 790 specimens. The acronyms used in the present study refer to the following collections (relevant curators/collection managers are acknowledged in parentheses):

DBUC	Department of Biological, Geological and Environmental Sciences, University of Catania, Italy
FMNH	Field Museum of Natural History, Chicago, U.S.A. (J. Boone)
JEBC	Colección Entomológica Y Museo Juan Enrique Barriga-Tuñón, Curicó, Chile (J. E. Barriga-Tuñón)

MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France (T. Deuve and A. Taghavian)
MNHS	Museo Nacional de Historia Natural, Santiago, Chile (M. Elgueta Donoso and Y. J. Sepulveda Guaico)
MSNG	Museo Civico di Storia Naturale "G. Doria", Genova, Italy (R. Poggi)
NHMW	Naturhistorisches Museum, Wien, Austria (H. Schillhammer)
PHPC	Private collection of Peter Hlavác, Prague, Czech Republic (P. Hlavác)
UNHC	University of New Hampshire Arthropod Collection, Durham, NH, U.S.A. (D.S. Chandler)

Under the sections "type material" or "additional material" the locality data are standardized, with indications of major administrative units (regions and provinces) and names of collectors; for the holotypes of older specimens the labels are also given verbatim. For the method of selection of the type material see Sabella *et al.* (2017).

Images were taken using a Leica DFC425 camera in conjunction with a Leica M205-C compound microscope. Zerene Stacker (version 1.04) was used for image stacking. All images were modified and grouped using Adobe Photoshop and Illustrator CS6.

The body length is measured from the anterior clypeal margin to the posterior margin of the last visible abdominal tergite. The length and width of the body parts were measured between points of maximum extension, *e.g.* the head length is measured between the anterior clypeal margin and the posterior margin of the neck; the head width includes the eyes, the elytral length along the suture line, and the elytral width is the total width of the two elytra taken together. The abdominal tergites are numbered based on order of visibility. Morphological terminology follows that of Chandler (2001), except our use of "ventrite" instead of "sternite" when describing meso- and metathoracic structures, and that the sclerotized features of the dorsal plate of the aedeagus termed "dorsal strips" in Sabella *et al.* (2017) are here termed "longitudinal struts".

TAXONOMY

Achilia approximans and *A. puncticeps* species groups

Reitter (1883: 51, pl. I fig. 10) described and illustrated the new species *Bryaxis puncticeps* on the basis of a single specimen from Valdivia, that he considered to be a female. Two years later he described and illustrated the male of *B. puncticeps* (Reitter, 1885: 324, 326, pl. II fig. 5), as well as the new species *B. approximans* (Reitter, 1885: 324, 326, pl. II fig. 4) based on a single female from Valdivia, two taxa he transferred subsequently to *Achilia*

(Reitter, 1890). Then Jeannel (1962: 414, figs 166-168) redescribed and illustrated the two sexes of *A. puncticeps* based on the specimens identified as such by Reitter, as well as the male of *A. approximans* (Jeannel, 1962: 437, figs 212-213), placing each of these two taxa in its own species group.

However our study of the types of these two taxa led us to conclude that *A. approximans* is a junior synonym of *A. puncticeps* (see comments under that species). It also appeared that Jeannel (1962) defined his *A. puncticeps* species group using mainly male features pertaining to a distinct, very different new species (see comments under *A. puncticeps*, and *A. zaurda* n. sp.). His concept of the *A. puncticeps* species group is thus chimeric and, to eliminate confusion, we will therefore consider his *A. approximans* species group to consist solely of *A. puncticeps*.

According to Jeannel (1962: 398, 437) the *A. approximans* species group, which was thus defined using features pertaining to true males of *A. puncticeps*, is characterized by: 3 elytral basal foveae; basal striae of abdominal tergite I separate at most by 1/4 of tergal width; anterior portion of the front of the male flattened and pubescent; antennomeres of male unmodified with those from 3 to 8 distinctly wider than long; distal edge of parameres of aedeagus not denticulate, internal sac with three or four macrospines. However, besides that the characters defining the *A. approximans* species group were extrapolated from the only included species, some of them were also incorrectly observed, such as the number of elytral basal fovea which are 4 instead of 3.

As mentioned in the introduction our research plan is to investigate the phylogenetic significance of morphological characters within *Achilia* only after completing a thorough assessment of its diversity, and therefore we prefer here to refrain from redefining Jeannel's species groups, or propose new ones. Nevertheless, in the extensive material examined so far, we have recognized six new species – *i.e.* *A. adorabilis* n. sp., *A. baburra* n. sp., *A. cunniceps* n. sp., *A. nipponobythoides* n. sp., *A. reitteri* n. sp. and *A. trulla* n. sp. – resembling *A. puncticeps* closely with respect to several external male characters and the conformation of their aedeagi to justify inclusion of their descriptions in this paper. These seven species share in common the following unique set of characters: pubescence decumbent, consisting of long setae uniform over entire body; head wider than long; pronotum wider than long; anterior portion of lateral margins of pronotum convergent, posterior portion subparallel and sinuate; pronotal disc slightly convex, smooth and shiny with some punctures; basal margin of pronotum bordered with row of contiguous shallow impressions; elytra together wider than long, with protruding humeri; elytral disc smooth, shiny, with punctures; presence of four basal foveae (two lateral foveae very close); sutural stria entire; discal stria extending to about elytral midlength; abdomen smooth, with some minute punctures; basal

striae of first abdominal tergite separate at least by one-quarter of tergal width; first tergite with short and sparse setal brush between diverging basal striae; aedeagus with dorsal plate ovoid, and dorsal longitudinal struts divergent; ventral lamina with upper margin bent anteriorly and forming apically two short lateral spines (this lamina lacking in *A. baburra*); internal sac with pair of long medial sclerites recurved and strongly sclerotized at base (except *A. baburra* in which the medial sclerites are fused, and *A. cunniceps* in which the medial sclerites end apically with 5-6 spines), associated on each side with other sclerites, different in form and number in each species. Parameres thin and curved inwards, bearing three long subapical setae (except in *A. trulla* in which there are four).

In order to keep the text more concise, these features are not repeated in their respective descriptions.

The specimens matching the males identified and illustrated as those of *A. puncticeps* by Reitter (1885) and Jeannel (1962) are described at the end of this paper (i.e. *A. zaurda* n. sp.).

Achilia puncticeps (Reitter, 1883)

Figs 1, 13, 25, 29-30, 57

Bryaxis puncticeps Reitter, 1883: 51, pl. I fig. 10 (head and antennae).

Achilia puncticeps. – Jeannel, 1962: 414-415 (pro parte, description of female) fig. 167 (head and antennae).

Bryaxis approximans Reitter, 1885: 324, 326, pl. II fig. 4 (head and antennae) (**syn. nov.**).

Achilia approximans. – Jeannel, 1962: 437, figs 212 (head and antennae) and 213 (aedeagus).

Type material (2 ex.): MNHN (ex coll. Raffray); 1 ♂ (holotype of *Achilia puncticeps*); Chili; labels verbatim “Type / Chili / Muséum de Paris, 1917, coll. A. Raffray / *A. puncticeps*, A. Raffray det. / *puncticeps* Reitt. (handwritten by Jeannel) / female symbol”. – MNHN (ex coll. Raffray); 1 ♀ (holotype of *Achilia approximans*): CENTRAL CHILI: Región Los Ríos: Valdivia prov.: labels verbatim “Type / *B. approximans* m., Valdivia (handwritten by Reitter) / Muséum de Paris, 1917, coll. A. Raffray / *A. approximans*, A. Raffray det. / *approximans* Reitt. (handwritten by Jeannel)”.

Additional material examined (70 ex.): MNHN (coll. Raffray); 3 ♂; Chili. – SOUTHERN AND CENTRAL CHILI: Región Aysén: Aysén prov.: MHNG; 1 ♂; Rio Simpson National Park, 33 km E Puerto Aysén; 70 m; 26.I.1985; S. & J. Peck; forest, sifted moss on stumps. – MHNG; 1 ♂ and 1 ♀; 30 km N Puyuhuapi, station 107; 100 m; 29.I.1985; S. & J. Peck; sifted moss on logs. – MNHG; 8 ♂; 15 km S Las Juntas, 30 km N Puyuhuapi; 100 m; 30.XII.1984/29.I.1985; S. & J. Peck; FIT, *Nothofagus* forest. – Región Los Lagos: Palena prov.: FMNH (FMHD #85-991, #85-108); 1 ♂; 4 km

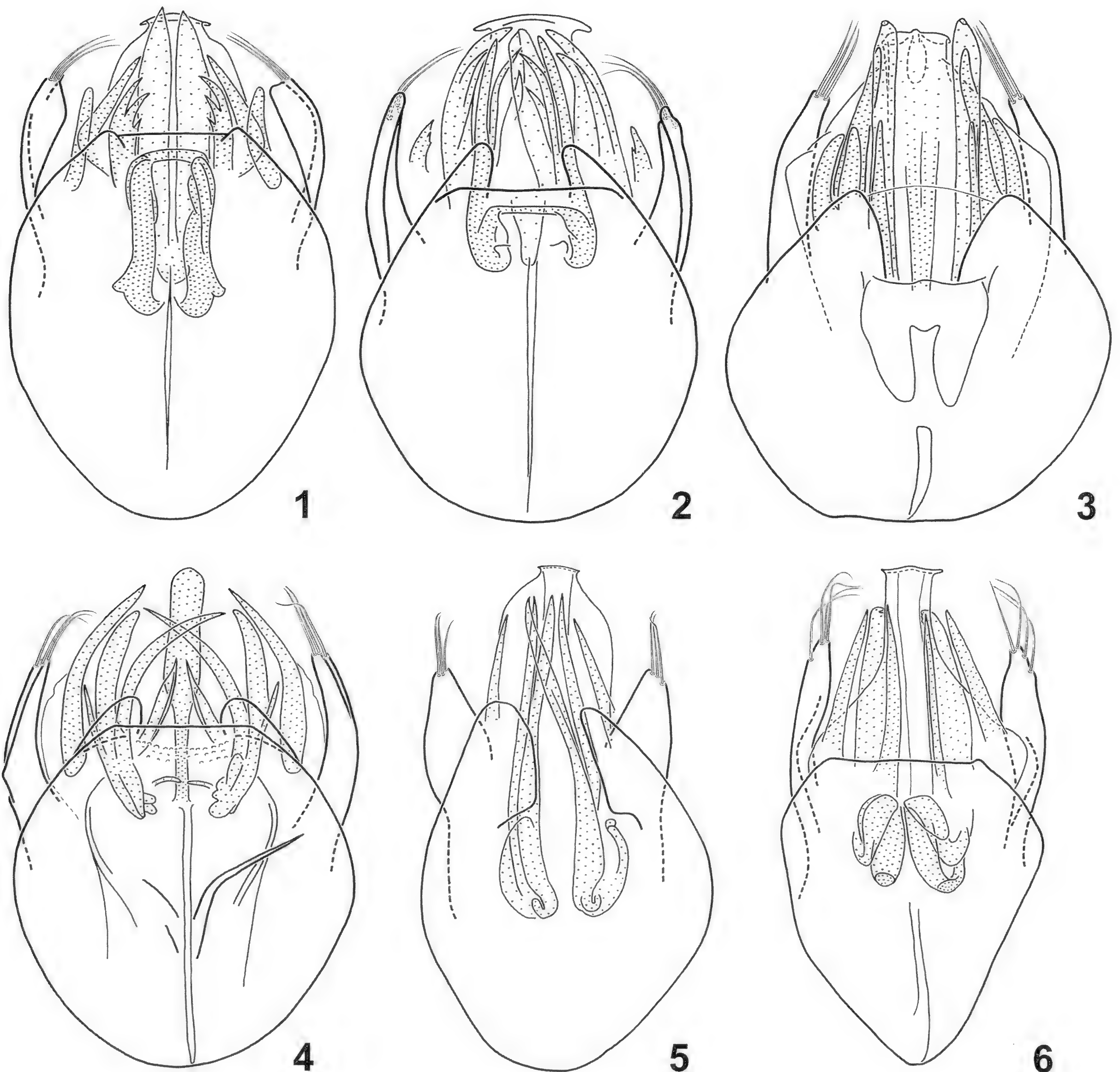
NW Chaiten; 10 m; 30.I.1985; S. & J. Peck; mixed forest litter, sooty fungus, Berlese. – Llanquihue prov.: MNHN (coll. Raffray, sub *A. approximans*); 1 ♂ and 2 ♀; Los Riscos; 41° 13'S; 11.IV.1954; G. Kuschel. – MNHS; 2 ♀; same data. – FMNH; 2 ♂; Lago Chapo, 13.5 km E Correntoso, site 656; 310 m; 16-27.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, flight intercept (windows) trap. – UHNC; 3 ♂; same data. – FMNH; 1 ♂; same data, but Berlese, leaf & log litter, forest floor. – UHNC; 1 ♂; same data. – FMNH (FMHD #97-28); 2 ♂; Alerce Andino National Park, near Sargazo entrance, 11.4 km from Correntoso; 41° 30'S 72° 37'W; 350 m; 19.I.1997; A. Newton & M. Thayer 998; Valdivian rainforest, Berlese, leaf & log litter. – FMNH (FMHD #97-14); 3 ♂; Lago Chapo, near SE end, km 9.9 on road from Rollizo; 41° 30.63'S 72° 23.98'W; 385 m; 04-26.I.1997; A. Newton & M. Thayer 989; Valdivian rainforest on steep slope, flight intercept trap. – Chiloé prov.: MNSG; 2 ♂; Chiloé Island, Estero Llicaldad; TC-608; 19.I.2000; T. Cekalovic. – MHNG; 1 ♂; Chiloé National Park, near Cucao, 30 km SW Castro, station 34b; 42° 37'S 74° 08'W; 10-70 m; 28.XII.1992/01.I.1993; D. Burckhardt; sifting of moss on forest floor trees and dead trunks and vegetational debris. – FMNH (FMHD #2002-72); 1 ♂; S side of Huillinco lake, road to Bellavista; 1.3 km S road of Cucao; 42° 41.81'S 73° 55.88'W; 45 m; 12-22. XII.2002; A. Newton & M. Thayer 1062; Valdivian rainforest w/emergent *Saxegothea conspicua*, flight intercept trap. – FMNH (FMHD #2002-066); 1 ♂; Quemchi, 11 km W of (11 km E Hwy 5); 42° 10.40'S 73° 35.73'W; 140 m; 10-21.XII.2002; A. Newton, M. Thayer & D. J. Clarke; Valdivian rainforest remnant w/thick bamboo understory; flight intercept trap. – FMNH (FMHD #97-24); 1 ♂; Colonia Yungay road to (3.6 km W Hwy 5); 42° 59'S 73° 41'W; 90 m; 17.I.1997; A. Newton & M. Thayer 995; grazed secondary Valdivian rainforest remnants, Berlese, leaf & log litter. – Osorno prov.: FMNH; 1 ♂; 7.7 km NE Termas de Puyehue, site 664; 200 m; 19-25.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, Berlese, leaf & log litter, forest floor. – FMNH (FMHD # 97-5); 1 ♂; Puyehue National Park, 4 km E Anticura; 40° 39.73'S 72° 08.10'W; 460 m; 30.I.1997; A. Newton & M. Thayer 985-3; Valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH; 4 ♀; Puyehue National Park, 4.1 km E Anticura, trap site 662; 430 m; 19-26.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, screen sweeping at dusk. – MHNG; 4 ♂ and 14 ♀; Puyehue National Park, Antillanca Road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting. – FMNH (FMHD #85-923, #85-38); 1 ♂; same data. – FMNH; 1 ♂; Chincay, 10 km E of Bahía Mansa; 50 m; 21.XII.1982; A. Newton & M. Thayer; 2nd Valdivian forest, Berlese, leaf & log litter, forest floor. – Región Los Ríos: Valdivia prov.: JEBC; 2 ♂; Valdivia, Chaihuin, Camino a Huaicolla;

S 39° 59.926' W 73° 38.976'; 107 m; 12.I.2007; J.E. Barriga-Tuñón; fogging *Nothofagus dombeyi*. – JEBC; 1 ♀; Valdivia, Parque Oncol, casa visitas; S 39° 42.303' W 73° 18.704'; 473 m; 07.I.2007; J.E. Barriga-Tuñón; fogging s/ *Nothofagus pumilio*. – FMNH; 1 ♂; 4.1 km W Anticura, site 663; 270 m; 19-25.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, flight intercept (windows) trap. – UHNC; 1 ♂; same data. – MHNG; 1 ♂; Alerce Costero National Park, near Chaihuin; 0-100 m; 16.II.2018; S. Kurbatov; forest litter. – MHNG; 1 ♂; Alerce Costero National Park, near Chaihuin; 500 m; 15.II.2018; G. Sabella & D. Mifsud; forest litter.

Description: Body 1.30-1.45 mm long, entirely dark

brown with reddish elytra darker at base and along sutural stria; antennae, palpi and legs reddish-brown. Head with vertexal sulcus deeply impressed; eyes moderately protruding, shorter than slightly convex temples. Pronotum as wide as head; median antebasal fovea as large as lateral ones. First abdominal tergite with basal striae extending to about one-quarter of paratergal length, and separated at base by about one-quarter of tergal width.

Male: Head as in Figs 29-30; frons flattened, densely punctate and pubescent, disc with broad V-shaped impression with distinctly raised margins; frontal lobe short and raised. Antennae (Fig. 13) with scape and pedicel longer than wide; all funicular antennomeres



Figs 1-6. Aedeagi of *Achilia* species. (1) *A. puncticeps*. (2) *A. reitteri* n. sp. (3) *A. adorabilis* n. sp. (4) *A. baburra* n. sp. (5) *A. nipponobythoides* n. sp. (6) *A. trulla* n. sp.

wider than long, except antennomere V as long as wide; antennomeres IX and X strongly transverse with protruding mesal margins; antennomere XI very elongate and distinctly longer than VI-X combined, bearing long and thin subbasal seta inserted in deep impression, its surface with some tubercles. Metaventrite raised at middle, this area with some fine punctures, distally pubescent and divided by wide median longitudinal sulcus. Legs with trochanters very elongate; surface of protrochanters and mesotrochanters bearing numerous long bristles; ventral margin of mesotrochanters projecting posteriorly in a spine (Fig. 25); profemora and mesofemora slightly thickened; distal half of mesotibiae slightly sinuate and with long and thick bristles; distal half of metatibiae slightly sinuate. Abdominal tergites and ventrites unmodified. Aedeagus (Fig. 1, dorsal longitudinal struts not shown) 0.26-0.29 mm long, medial sclerites apically pointed, and associated on each side with three pointed sclerites, the proximal trifid.

Female: Similar to male except: head with frons slightly convex (not flattened) without punctures, and with large vertexal fovea beside each eye; antennae shorter and thinner than male; metaventrite and legs unmodified.

Collecting data: Collected from December to April, mainly in Valdivian rainforests, but also in *Saxegothaea* forests, where it was found in remnants and in boundary forests at elevations ranging from sea level to 1000 m. Most specimens came from flight intercept traps but also by sifted samples of leaf and log litter, moss, dead trunks, vegetable debris and mushrooms, and by car netting.

Distribution: *Achilia puncticeps* is known from Southern and Central Chile (Fig. 57: red circles), ranging from Aysén to Valdivia provinces.

Comments: Our study of the types of *A. puncticeps* and *A. approximans*, as well as those specimens identified as such by Reitter (1883, 1885) and Jeannel (1962), revealed that the “female” holotype of *A. puncticeps* is indeed a male conspecific with the female holotype of *A. approximans*. Consequently *A. approximans* (Reitter, 1885) is here placed as a junior synonym of *A. puncticeps* (Reitter, 1883) (**syn. nov.**). It also appeared that the males identified and illustrated as pertaining to *A. puncticeps* by Reitter (1885: 324, 326, pl. II, fig. 5) and Jeannel (1962: 414, figs 166-168) belong indeed to a quite different species, which is described as new at the end of this paper (i.e. *A. zaurda* n. sp.). See also the previous section dedicated to the definition of the *A. puncticeps* species group.

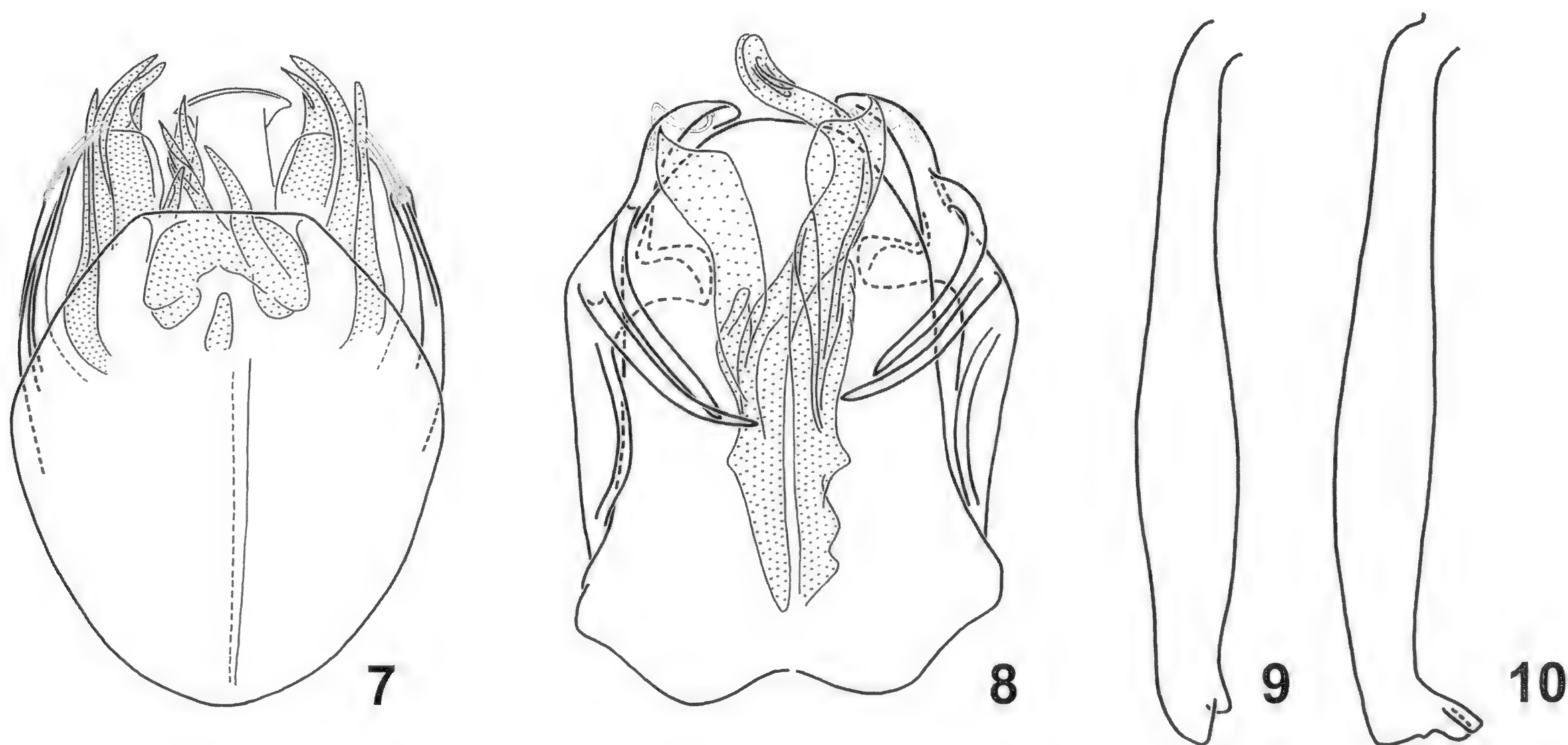
Achilia puncticeps can be distinguished from the other members of the genus by the morphology of the male head (Figs 29-30), features of the antennae (Fig. 13), and the copulatory pieces of the aedeagus (Fig. 1).

***Achilia reitteri* n. sp.**

Figs 2, 9, 14, 21, 31-32, 57

Holotype: MHNG (# MHNG-ENTO-1383); 1 ♂; SOUTHERN CHILI: Región Los Lagos: Osorno prov.: Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting.

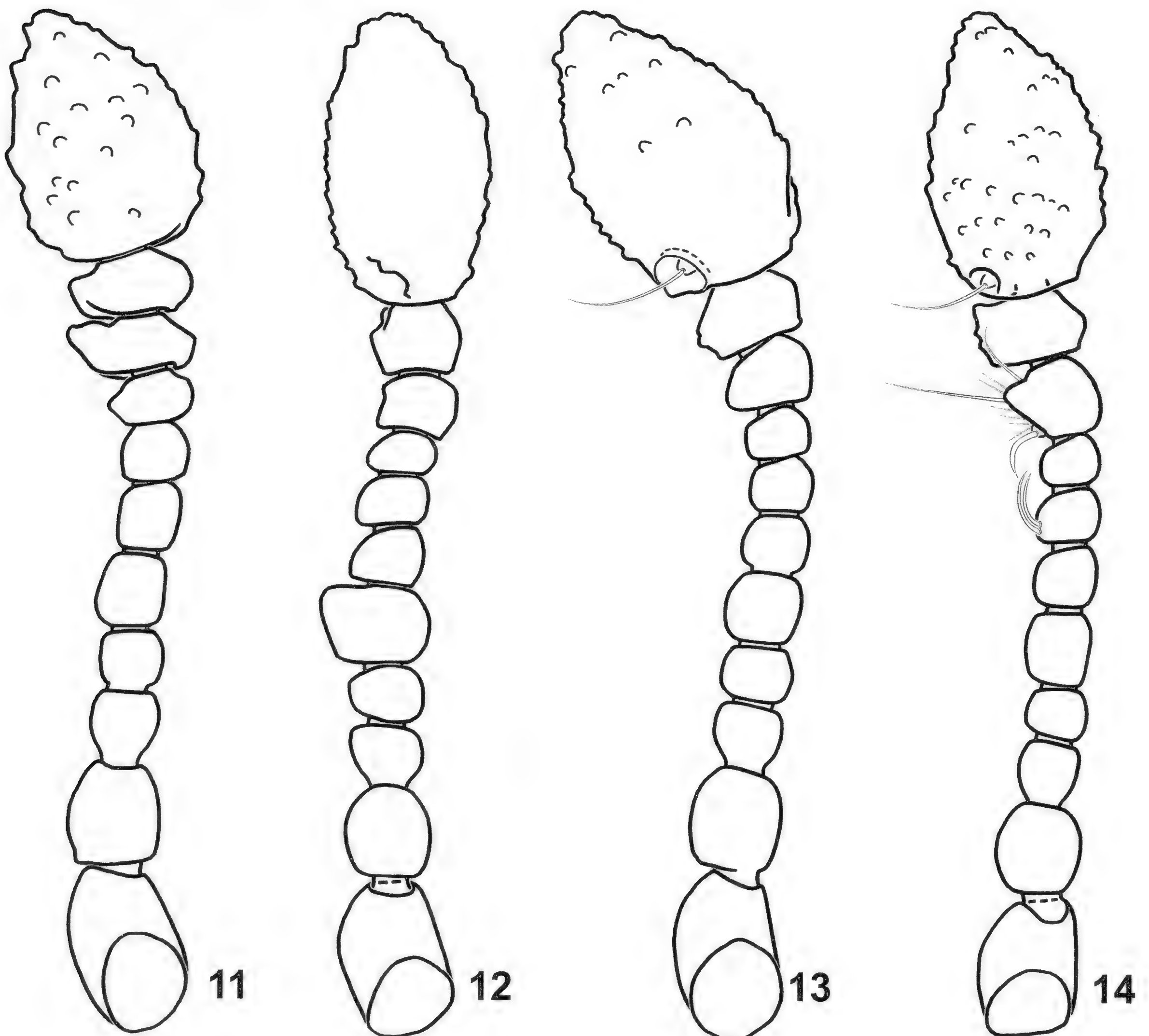
Paratypes (96): SOUTHERN AND CENTRAL CHILI: Región Aysén: Aysén prov.: MHNG; 1 ♂; 16 km NW Cisnes Medio, Río Grande; 200 m; 30.XII.1984-28.I.1985; S. & J. Peck; FIT mature beech forest. – MHNG; 1 ♂; Rio Simpson National Park, 33 km E Puerto Aysén; 70 m; 31.XII.1984/26.I.1985; S. & J. Peck; FIT, select cut forest. – Región Los Lagos: Llanquihue prov.: UNHC; 1 ♂; Salto Petrohué, 6.4 km



Figs 7-10. Aedeagi (7-8) and mesotibiae (9-10) of *Achilia* species. (7) *A. cunniceps* n. sp. (8, 10) *A. zaurda* n. sp. (9) *A. reitteri* n. sp.

SW Petrohué; 140 m; 28.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, Berlese, leaf & log litter, forest floor. – FMNH; 1 ♂; Lago Chapo, 13.5 km E Correntoso, site 656; 310 m; 16-27.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, flight intercept (windows) trap. – FMNH; 1 ♀; same data, but Berlese, leaf & log litter, forest floor. – Chiloé prov.: FMNH; 1 ♂; Ahoni Alto; 70 m; 22.II.1988; L. Masner, primary forest. – Osorno prov.: UNHC; 1 ♂; 7.7 km NE Termas de Puyehue, site 664; 200 m; 19-25.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, Berlese, leaf & log litter, forest floor. – FMNH (FMHD #85-923, #85-38); 3 ♂; Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting. – MHNG; 24 ♂ and 38 ♀; same data. – MHNS, 1 ♂ and 1 ♀; same data. – FMNH; 3 ♂ and 3 ♀; Puyehue National Park, Antillanca road, site 659;

720 m; 18-24.XII.1982; A. Newton & M. Thayer; *Nothofagus* spp. forest, flight intercept. – UNHC; 2 ♂ and 2 ♀; same data. – FMNH; 1 ♀; Puyehue National Park, Antillanca road; 470-720 m; 18-24.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, screen sweeping at dusk. – MHNG; 5 ♂; Puyehue National Park, Antillanca road; 600-1000 m; 20.XII.1984; S. & J. Peck; car netting. – MHNG; 1 ♂; Puyehue National Park, Aguas Calientes; 500 m; 20.XII.1984; S. & J. Peck; forest litter on trail, sifting. – MHNG; 1 ♂; Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; D. Agosti & D. Burckhardt. – FMNH (FMHD # 97-5); 1 ♂; Puyehue National Park, 4 km E Anticura; 40° 39.73'S 72° 08.10'W; 460 m; 30.I.1997; A. Newton & M. Thayer 985-3; Valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – Región Los Ríos: Valdivia prov.:

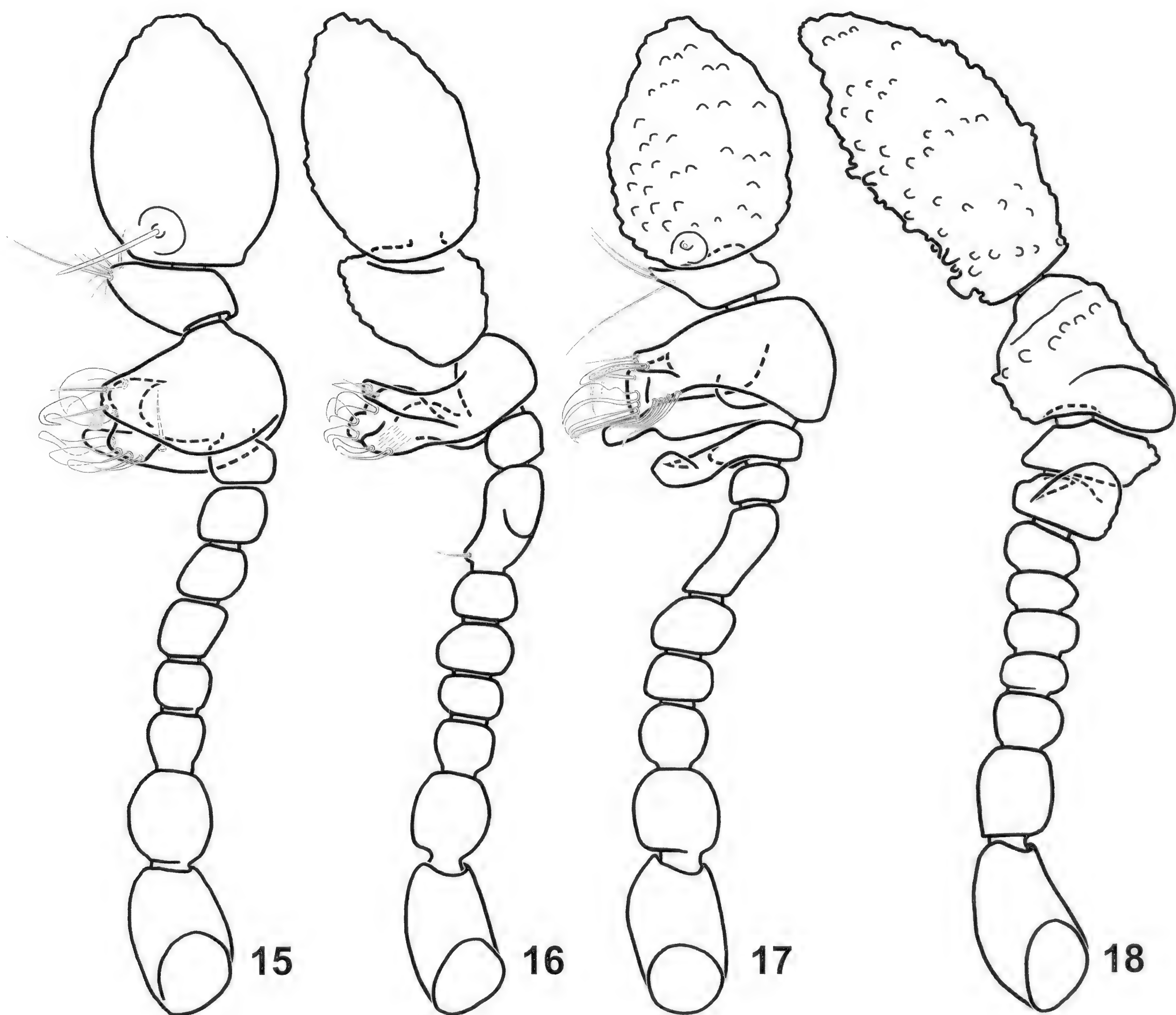


Figs 11-14. Antennae of *Achilia* species. (11) *A. cunniceps* n. sp. (12) *A. baburra* n. sp. (13) *A. puncticeps*. (14) *A. reitteri* n. sp.

MHNG; 1 ♂; Alerce Costero National Park, near Chaihuin; 500 m; 15.II.2018; G. Sabella & D. Mifsud; forest litter. – Región Araucanía: Malleco prov.: MHNG; 1 ♂; Puren, Contulmo Natural Monument; 350 m; 11.XII.1984-13.II.1985; S. & J. Peck 85-16; FIT, mixed evergreen forest & MT *Nothofagus*. – Región Bío Bío: Concepción prov.: MSNG; 1 ♂; El Manzano; TC-189; 03.I.1988; T. Cekalovic.

Description: Body 1.30-1.40 mm long, entirely dark brown with reddish elytra darker at base and along sutural stria; antennae, palpi, and legs reddish-brown. Head with eyes moderately protruding, distinctly shorter than slightly convex temples. Pronotum as wide as head; median antebasal fovea as large as lateral ones. First abdominal tergite with basal striae extending to about one-quarter of paratergal length, and separated at base by more than one-quarter of tergal width.

Male: Head as in Figs 31-32; frons flattened, densely punctate and pubescent, disc with broad V-shaped depression with distinctly raised margins; vertexal sulcus shallowly impressed; frontal lobe wide and flattened. Antennae (Fig. 14) with scape and pedicel longer than wide; antennomere III as long as wide, antennomere IV wider than long; antennomere V longer than wide, antennomeres VI-VIII wider than long, VII bearing two long setae on its mesal margin; antennomere IX transverse with protruding distal mesal margin and bearing setae on its mesal margin; antennomere X strongly transverse: antennomere XI very elongate and distinctly longer than VI-X combined, bearing long and thin subbasal seta inserted in deep impression, its surface with many tubercles. Metaventricle raised at middle, this area with some fine punctures, distally pubescent, and divided by wide median sulcus. Legs with trochanters very elongate;

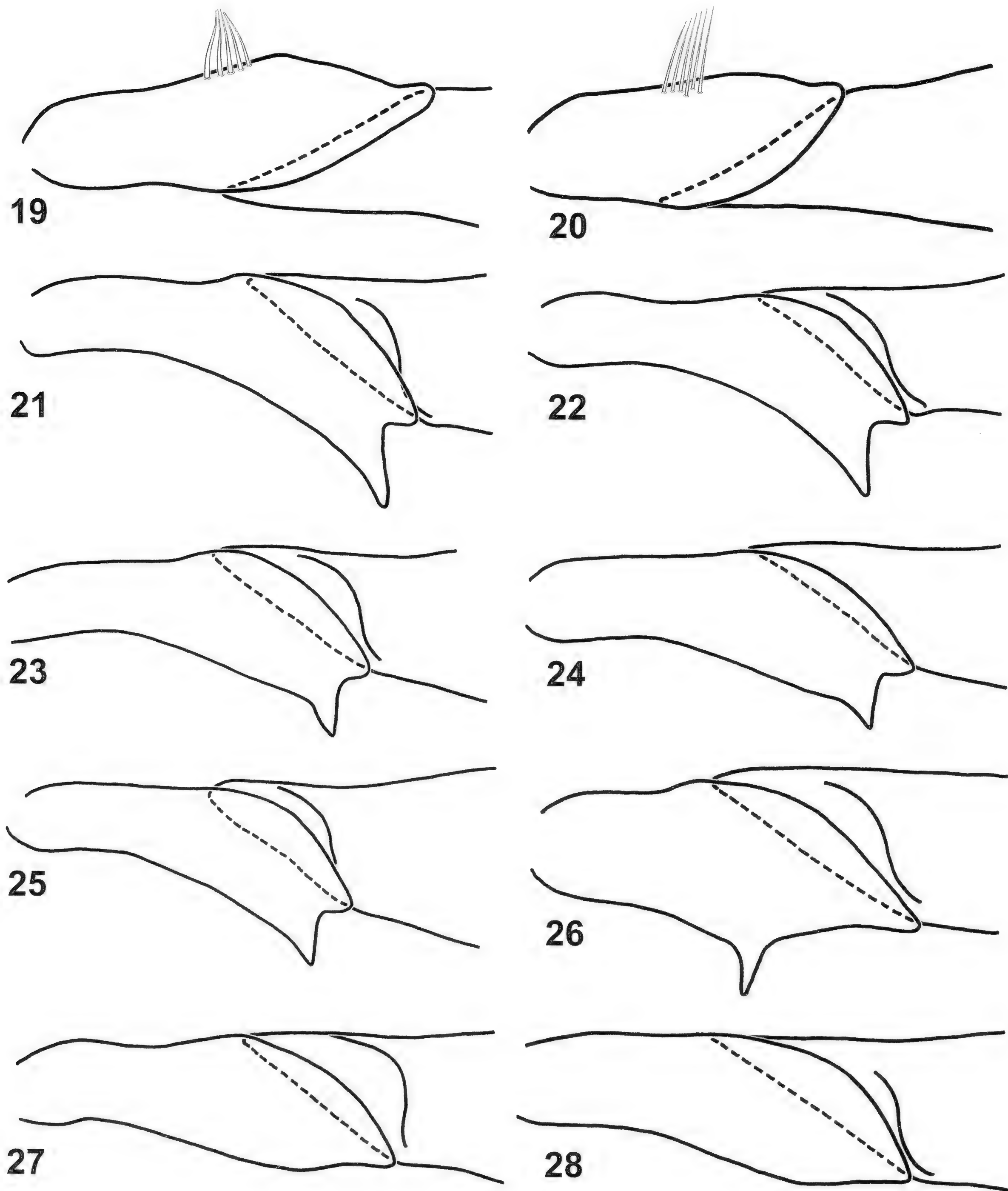


Figs 15-18. Antennae of *Achilia* species. (15) *A. nipponobythoides* n. sp. (16) *A. adorabilis* n. sp. (17) *A. trulla* n. sp. (18) *A. zaurda* n. sp.

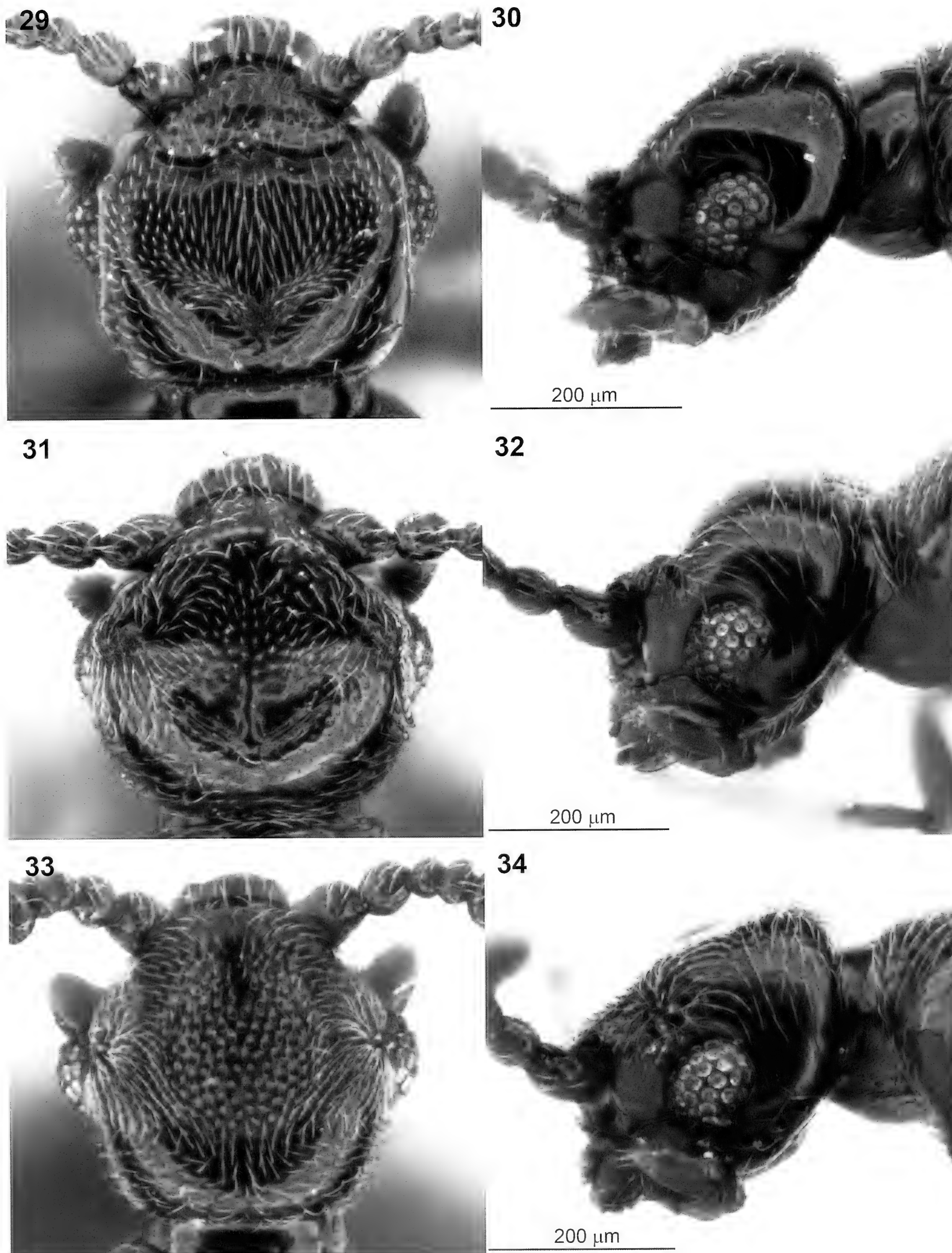
surface of protrochanters and mesotrochanters bearing numerous long bristles; ventral margin of mesotrochanters projecting posteriorly as spine (Fig. 21); profemora and mesofemora slightly thickened; mesotibiae with short subapical spur on medial margin (Fig. 9), distal half slightly sinuate bearing long and thick bristles and long and wide macroseta; distal half of metatibiae slightly

sinuate. Abdominal tergites and ventrites unmodified. Aedeagus (Fig. 2, dorsal longitudinal struts not shown) 0.27-0.30 mm long; long bifid medial sclerites associated on each side with four pointed sclerites.

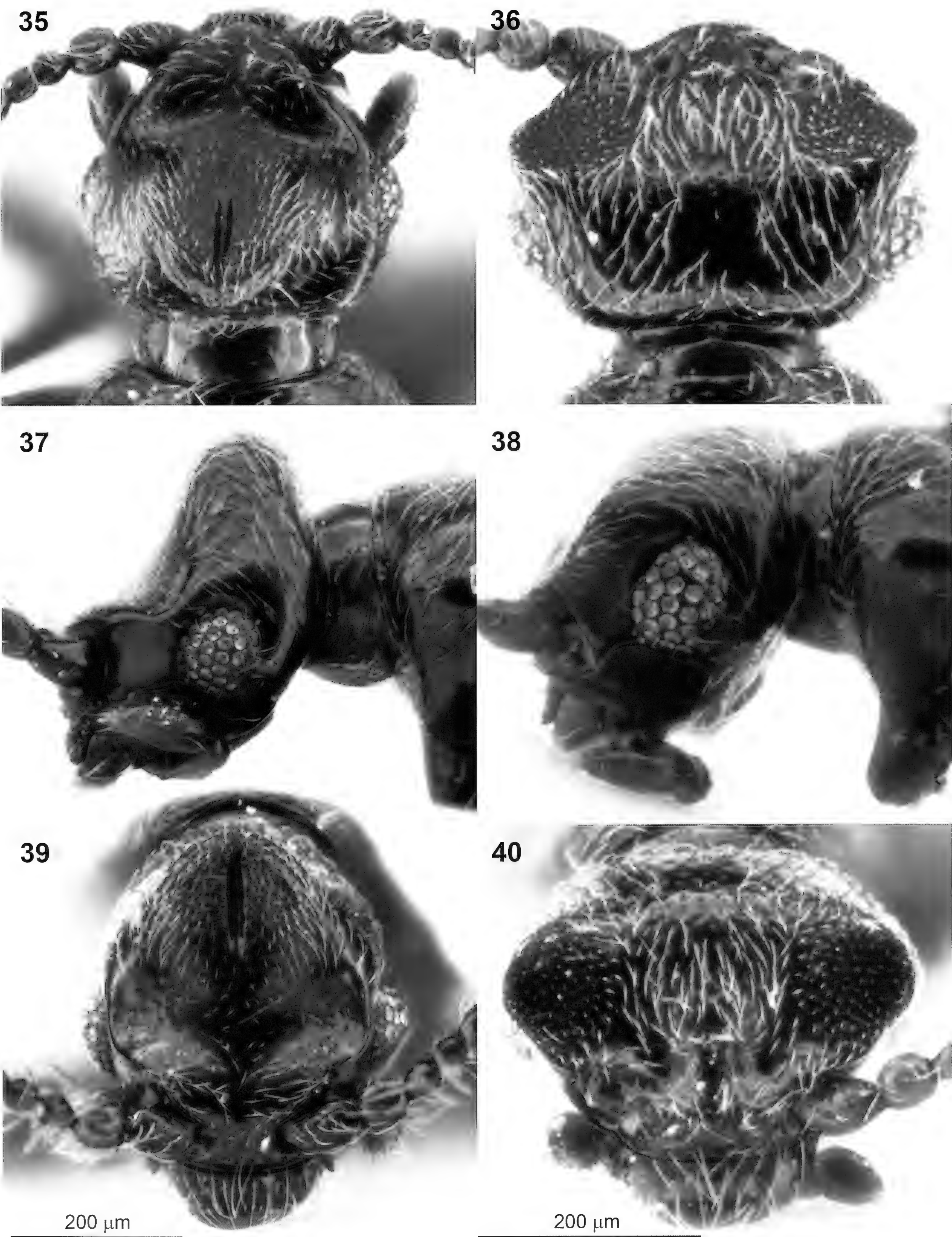
Female: Similar to male except: head with frons slightly convex (not flattened) without punctures and with large vertexal fovea beside each eye; vertexal sulcus present,



Figs 19-28. Protrochanters (19-20) and mesotrochanters (21-28) of *Achilia* species. (19, 22) *A. baburra* n. sp. (20, 28) *A. nipponobythoides* n. sp. (21) *A. reitteri* n. sp. (23) *A. cunniceps* n. sp. (24) *A. trulla* n. sp. (25) *A. puncticeps*. (26) *A. zaurda* n. sp. (27) *A. adorabilis* n. sp.



Figs 29-34. (29-30) *Achilia puncticeps*. (31-32) *A. reitteri* n. sp. (33-34) *A. baburra* n. sp. Male head in (29, 31, 33) dorsal and (30, 32, 34) lateral views.



Figs 35-40. (35, 37, 39) *Achilia cunniceps* n. sp. (36, 38, 40) *A. nipponobythoides* n. sp. Male head in (35-36) dorsal, (37-38) lateral and (39-40) frontal views.

well-impressed; antennae shorter and thinner than male; metaventrite, and legs unmodified.

Collecting data: Collected from December to February, mainly in Valdivian rainforests, at elevations ranging from 70 m to 1000 m. Most specimens came from car netting and flight intercept traps, but also by sifted samples of leaf and log litter.

Distribution: *Achilia reitteri* n. sp. is known from Southern and Central Chile (Fig. 57: green diamonds), ranging from Aysén to Concepción provinces.

Comments: *Achilia reitteri* n. sp. is similar to *A. puncticeps* from which it is easily distinguished by the male features of the head (compare Figs 29-30 and 31-32), antennae (compare Figs 13 and 14), mesotrochanters (compare Figs 21 and 25), and the copulatory pieces of the aedeagus (compare Figs 1 and 2). The females of the two species are distinguished because *A. puncticeps* has the sides of the frontal lobe clearly narrowed (slightly narrowed in *A. reitteri* n. sp.)

***Achilia cunniceps* n. sp.**

Figs 7, 11, 23, 35, 37, 39, 57

Holotype: MHNG (# MHNG-ENTO-13837); 1 ♂; SOUTHERN CHILI: Región Los Lagos: Osorno prov.: Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting.

Paratypes (3): MHNG (# MHNG-ENTO-13838 & 13839); 2 ♂; SOUTHERN CHILI: Región Los Lagos: Osorno prov.: same data as holotype. – Chiloé prov.: FMNH (FMHD #2002-77); 1 ♂; road to Miraflores, about 0.6 km W road 5; 42° 46.74'S 73° 47.70'W; 130 m; 12.XII.2002; A. Newton & M. Thayer 1063; secondary Valdivian forest with few conifers, Berlese, leaf & log litter.

Description: Body 1.35-1.40 mm long, entirely dark with reddish brown elytra, antennae, palpi, and legs. Head with eyes moderately protruding, about long as convex temples. Pronotum slightly wider than head; median antebasal fovea smaller than lateral ones. First abdominal tergite with basal striae extending to about one-third of paratergal length, and separated at base by about one-third of tergal width.

Male: Head as in Figs 35, 37, 39, with anterior part flattened; vertexal sulcus indistinct; posterior part conspicuously raised, strongly convex in lateral view (Fig. 37), this hump anteriorly flattened, densely punctate, pubescent, and sulcate medially. Antennae (Fig. 11) with scape longer than wide and pedicel only slightly longer than wide; antennomeres III-IV and VII slightly wider than long; antennomeres V-VI longer than wide, antennomere VIII strongly transverse with mesal margin protruding at middle; antennomeres IX and X strongly transverse with protruding mesal

margins; antennomere XI very elongate and distinctly longer than VI-X combined, its surfaces with tubercles. Metaventrite raised at middle, this area distally pubescent and densely punctate, divided by very wide median sulcus. Legs with trochanters very elongate; surface of mesotrochanters bearing numerous long bristles; ventral margin of mesotrochanters projecting posteriorly in a spine (Fig. 23); profemora and mesofemora slightly thickened; protibiae with short subapical spur on medial margin, distal half slightly sinuate and bearing long and thick bristles; distal half of metatibiae slightly sinuate. Abdominal tergites and ventrites unmodified. Aedeagus (Fig. 7, dorsal longitudinal struts not shown) 0.26-0.27 mm long; medial sclerites with 5-6 apical spines, associated on each side with three pointed sclerites, the first with two tips.

Female: Unknown.

Collecting data: Collected in December, at elevations ranging from 130 to 1000 m, by car netting, and by sifting in Valdivian rainforests.

Distribution: *Achilia cunniceps* n. sp. is known from Southern Chile (Fig. 57: blue triangles) only in Región Los Lagos (Chiloé and Osorno provinces).

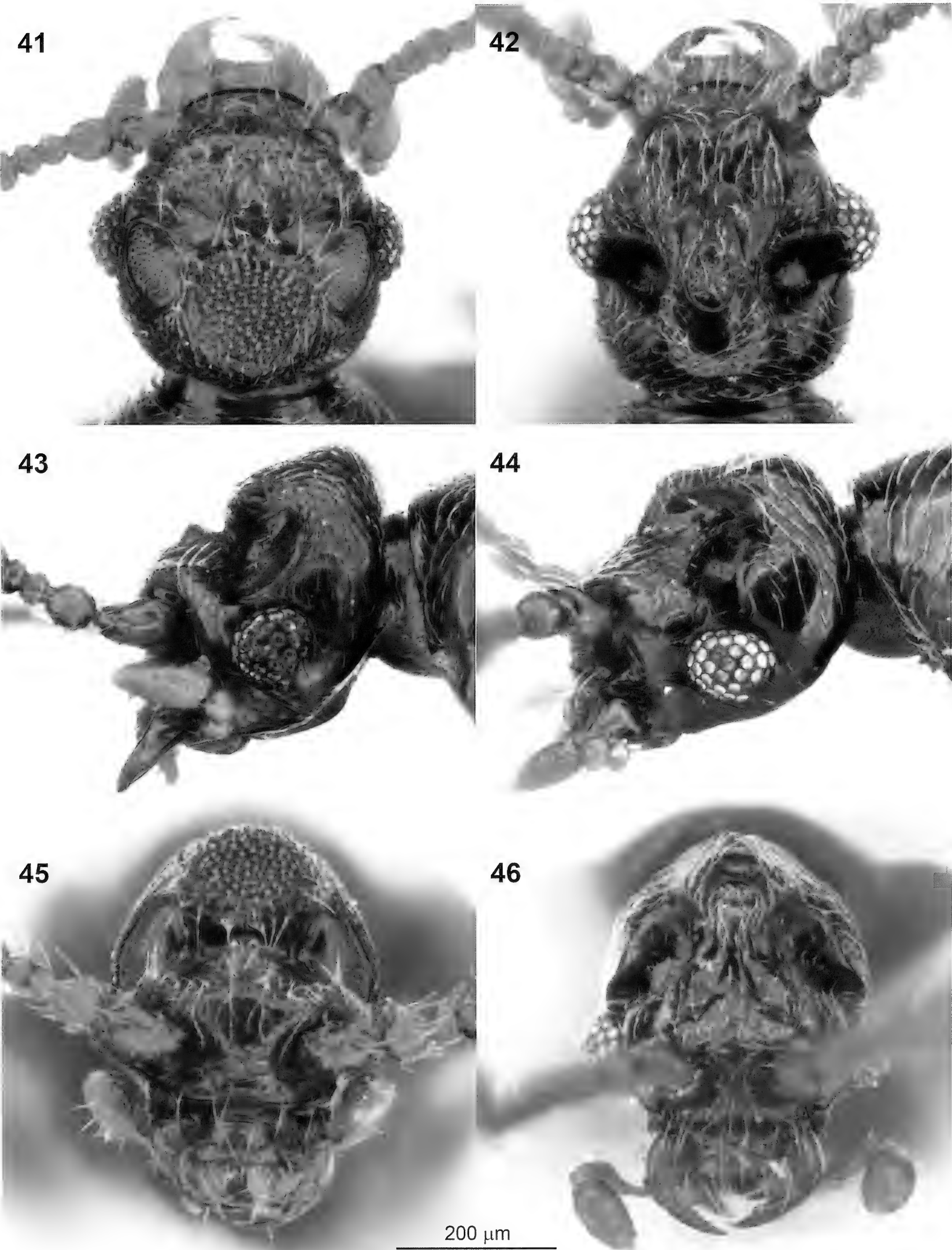
Comments: *Achilia cunniceps* n. sp. is easily distinguished from the other members of the genus by the very peculiar morphology of the male head (Figs 35, 37, 39), features of the antennae (Fig. 11), and the copulatory pieces of the aedeagus (Fig. 7).

***Achilia baburra* n. sp.**

Figs 4, 12, 19, 22, 33-34, 58

Holotype: MHNG (# MHNG-ENTO-13840); 1 ♂; SOUTHERN CHILI: Región Los Lagos: Osorno prov.: Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting.

Paratypes (99): SOUTHERN AND CENTRAL CHILI: Región Aysén: Aysén prov.: MHNG; 1 ♂; Rio Simpson National Park, 33 km E Puerto Aysén; 70 m; 31.XII.1984/26.I.1985; S. & J. Peck; FIT, select cut forest. – FMNH; 1 ♂; Rio Cisnes, 01-08.II.1958; L. Peña – Región Los Lagos: Llanquihue prov.: FMNH; 1 ♂; Salto Petrohué, 6.4 km SW Petrohué; 140 m; 28.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, Berlese, leaf & log litter, forest floor. – MHNG; 1 ♂; Vicente Perez National Park, Salto Petrohué; 150 m; 23.XII.1984/06.II.1985; S. & J. Peck; FIT, mixed moist forest. – Osorno prov.: MHNG; 2 ♂ and 1 ♀; Puyehue National Park, Aguas Calientes; 500 m; 20.XII.1984/08.II.1985; S. & J. Peck; FIT, derrumbes forest trail. – MHNG; 2 ♀; Puyehue National Park, road Aguas Calientes-Antillanca, station 19b; 40° 45'S 72° 15-20'W; 750-850 m; 30.XI/01.XII.1992; D. Burckhardt; sifting of moss on tree trunks and forest



Figs 41-46. (41, 43, 45) *Achilia adorabilis* n. sp. (42, 44, 46) *A. zaurda* n. sp. Male head in (41-42) dorsal, (43-44) lateral and (45-46) frontal views.

floor and vegetational debris. – MHNG; 1 ♀; Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; D. Agosti & D. Burckhardt. – FMNH (FMHD #85-923, #85-38); 2 ♂; Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting. – MHNG; 44 ♂ and 27 ♀; same data. – MHNS; 1 ♂ and 1 ♀; same data. – MHNG; 4 ♂; Puyehue National Park, Antillanca road; 600-1000 m; 18-20.XII.1984; S. & J. Peck; car netting. – FMNH; 1 ♂; 7.7 km NE Termas de Puyehue; site 664; 200 m; 19-25.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, Berlese, leaf & log litter, forest floor. – FMNH; 2 ♂; Puyehue National Park, Antillanca road, site 659; 720 m; 18-24.XII.1982; A. Newton & M. Thayer; *Nothofagus* ssp. forest, flight intercept (windows) trap. – UHNC; 3 ♂; same data. – FMNH; 1 ♂; Puyehue National Park, Antillanca road; 720-1000 m; 18-24.XII.1982; A. Newton & M. Thayer; *Nothofagus* ssp. forest, screen sweeping at dusk. – UHNC; 1 ♂; same data. – Región Los Ríos: Valdivia prov.: FMNH; 1 ♂; 4.1 km W Anticura, site 663; 270 m; 19-25.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, flight intercept (windows) trap. – FMNH (#97-5); 2 ♂; 4 km W Anticura; 460 m; 40° 39.73' S 72° 08.10' W; 01-30.I.1997; A. Newton & M. Thayer 985-3; Valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – Región Araucanía: Cautín prov.: FMNH; 1 ♂; Volcán Villarica, site 653; 1250 m; 15-29.XII.1982; A. Newton & M. Thayer; *Nothofagus dombey pumilio* w/*Chusquea*, Berlese, leaf & log litter, forest floor.

Description: Body 1.35-1.40 mm long, entirely dark brown with reddish elytra darker at base and along sutural stria; antennae, palpi and legs reddish-brown. Head with moderately protruding eyes shorter than slightly convex temples. Pronotum about as wide as head; median antebasal fovea smaller than lateral ones. First abdominal tergite with basal striae extending to about one-third of paratergal length, and separated at base by one-third of tergal width.

Male: Head as in Figs 33-34; frons densely punctate and pubescent, flattened from occipital region to frontal lobe, with distinctly raised margins; vertexal sulcus indistinct. Antennae (Fig. 12) with scape longer than wide and pedicel only slightly longer than wide; antennomeres III-IV distinctly transverse; antennomere V strongly transverse with protruding mesal margin; antennomeres VI-VIII transverse with protruding mesal margins; antennomeres IX and X transverse; antennomere XI very elongate and distinctly longer than VI-X combined. Metaventrite slightly raised at middle, with faint median sulcus. Legs with trochanters very elongate; ventral margin of protrochanters with a tuft of setae at middle (Fig. 19); mesotrochanters bearing numerous long bristles, with ventral margin projecting posteriorly as spine (Fig. 22); profemora and mesofemora slightly thickened; distal half of metatibiae slightly sinuate. Abdominal tergites and ventrites unmodified. Aedeagus

(Fig. 4) 0.26-0.28 mm long; medial sclerite enlarged in apical half, and associated on each side with two pointed sclerites, first with four spines.

Female: Similar to male except: head with frons slightly convex (not flattened) without punctures and with large vertexal fovea beside each eye; vertexal sulcus present and well-impressed, antennae shorter and thinner than male, antennomere V unmodified; metaventrite and legs unmodified.

Collecting data: Collected in December and January, mainly in Valdivian rainforest, at elevations ranging from 70 m to 1000 m. Most specimens came from car netting and flight intercept traps, but also by sifted samples of leaf and log litter.

Distribution: *Achilia baburra* n. sp. is known from Southern and Central Chile (Fig. 58: green diamonds), ranging from Aysén to Cautín provinces.

Comments: *Achilia baburra* n. sp. is similar to *A. puncticeps* from which it is easily distinguished by the male features of the head (compare Figs 33-34 and 29-30), the antennae (compare Figs 12 and 13), and the copulatory pieces of the aedeagus (compare Figs 1 and 4). The females of the two species are distinguished because *baburra* n. sp. has the frontal lobe longer and the temple more rounded than *A. puncticeps*.

***Achilia adorabilis* n. sp.**

Figs 3, 16, 27, 41, 43, 45, 51-53, 57

Holotype: MHNG (# MHNG-ENTO-13841); 1 ♂; SOUTHERN CHILE: Región Los Lagos: Osorno prov.: Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; D. Agosti & D. Burckhardt.

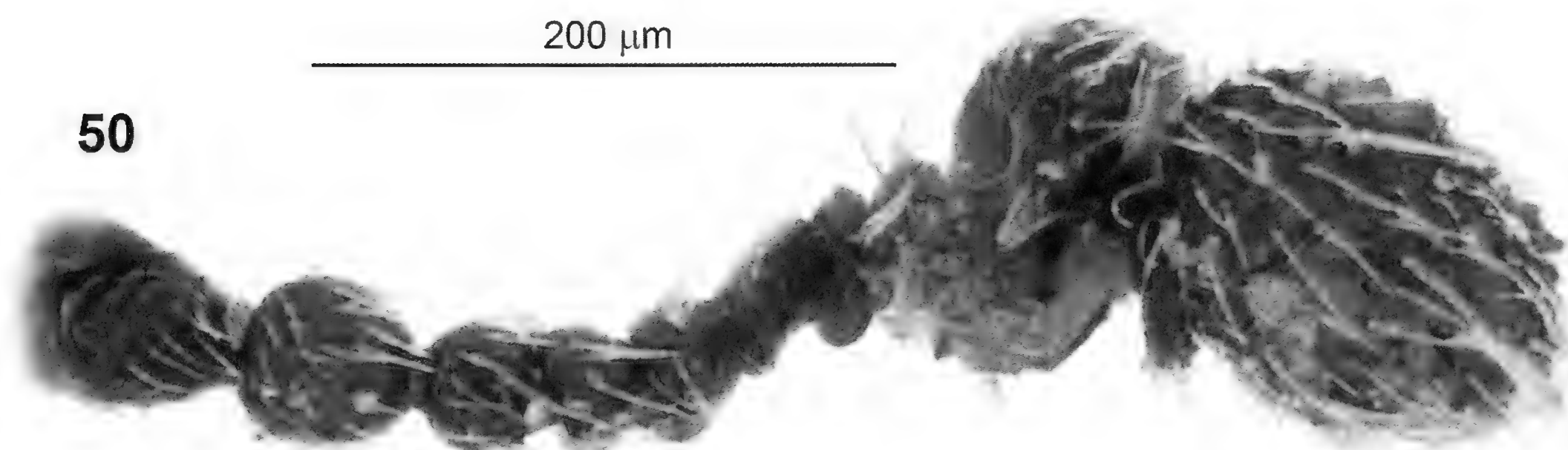
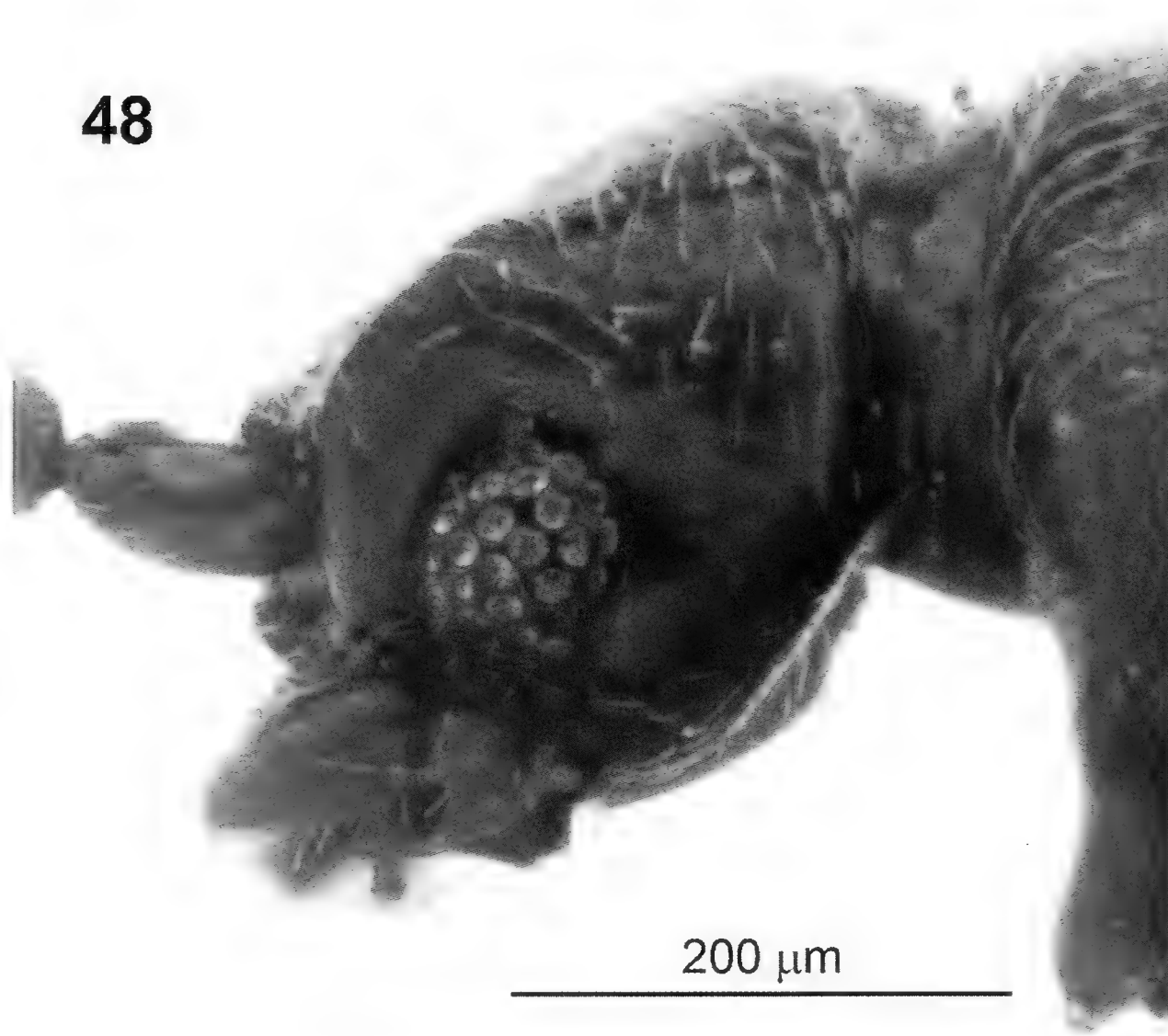
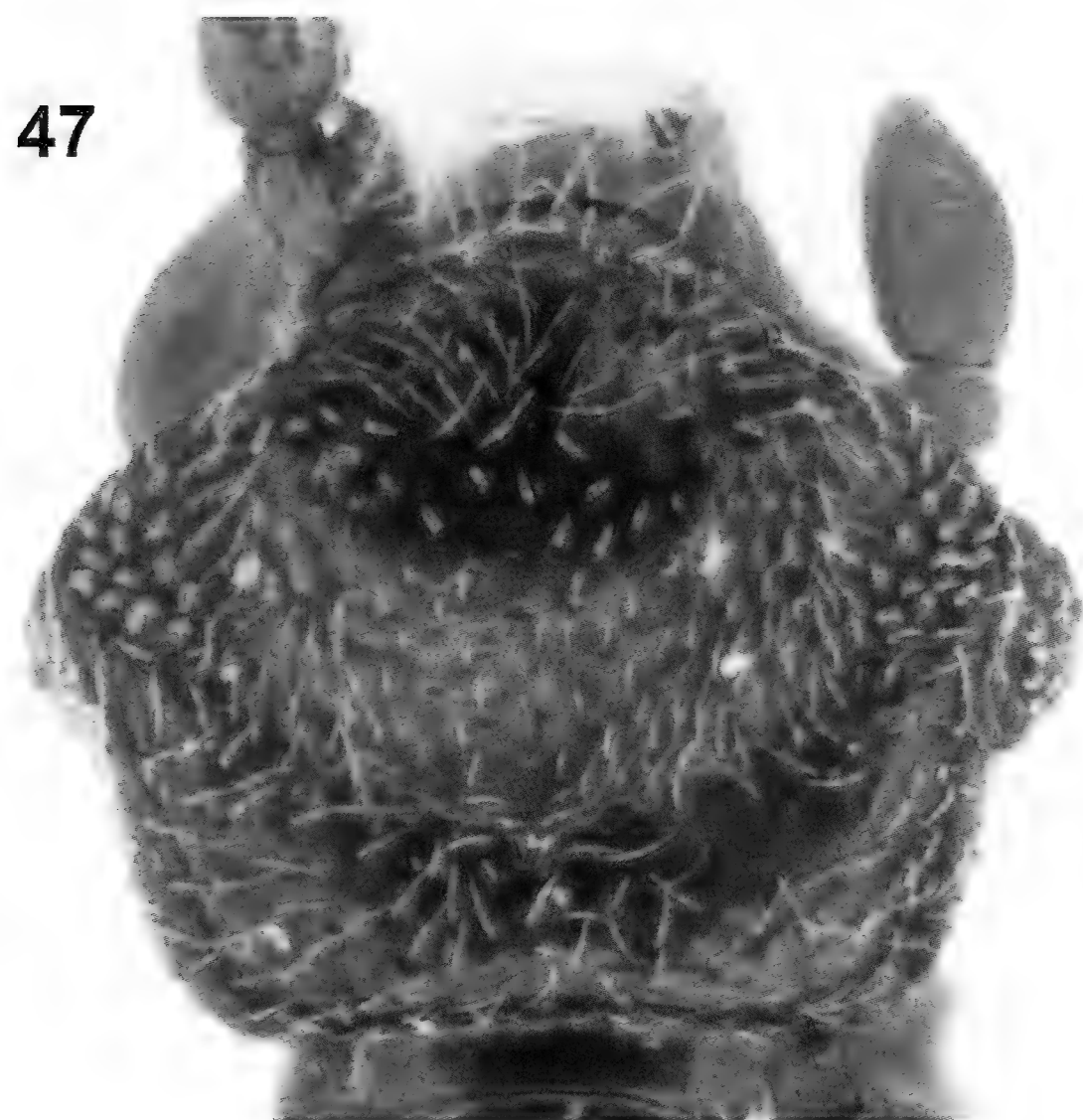
Paratypes (3): SOUTHERN CHILE: MHNG (# MHNG-ENTO-13842); 1 ♂; same data as holotype. – Región Aysén: Aysén prov.: MHNG (# MHNG-ENTO-13843 & 13844); 1 ♂ and 1 ♀; 16 km NW Cisnes Medio, Río Grande; 200 m; 30.XII.1984-28.I.1985; S. & J. Peck; FIT mature beech forest.

Description: Body 1.45-1.60 mm long, reddish-brown, with darker abdomen, reddish elytra, antennae and legs; palpi yellowish. Head with protruding eyes almost as long as convex temples. Pronotum slightly wider than head; median antebasal fovea smaller than lateral ones. First abdominal tergite with basal striae extending to about one-third of paratergal length, and separated at base by about one-third of tergal width.

Male: Head as in Figs 41, 43 and 45, with posterior half distinctly elevated at center, dorsally flattened and densely punctate, semicircular depression with finely punctate bottom on each side just above eyes; anterior part of head also elevated towards center forming two protuberances divided by carina, and separated from

posterior region by very deep and narrow transverse sulcus. Antennae (Figs 16, 51-53) with scape distinctly longer than wide and pedicel slightly longer than wide; antennomeres III-IV wider than long; antennomere V transverse with protruding mesal margin; antennomere VI slightly wider than long, antennomere VII about two times longer than wide with concave mesal margin bearing thin subbasal seta; antennomere VIII transverse;

antennomere IX only slightly wider than long, its mesal margin projecting in a long bilobed lamina bearing large apical setae; antennomere X very big and slightly longer than wide, its mesal margin distinctly protruding in the apical half; antennomere XI elongate and longer than VIII-X combined. Metaventricle raised at middle, this area depressed, punctate and densely pubescent. Legs with trochanters very elongate; mesotrochanters



Figs 47-50. *Achilia trulla* n. sp. Male head in (47) dorsal and (48) lateral views. Male left antenna in (49) dorsal and (50) frontal views.

(Fig. 27) unarmed; profemora and mesofemora slightly thickened; distal half of metatibiae slightly sinuate. Abdominal tergites and ventrites unmodified. Aedeagus (Fig. 3, dorsal longitudinal struts not shown) 0.35 mm long; medial sclerites apically rounded, and associated on each side with four pointed sclerites.

Female: Similar to male except: head unmodified with large vertexal fovea beside each eye; vertexal sulcus present; antennae, metaventrite, and legs unmodified.

Collecting data: Collected in December and January by flight intercept traps and by sifting in Valdivian rainforests.

Distribution: *Achilia adorabilis* n. sp. is known from Southern Chile (Fig. 57: yellow stars) only in Aysén and Los Lagos Regions.

Comments: *Achilia adorabilis* n. sp. is easily distinguished from the other members of the genus by the very peculiar morphology of the male head (Figs 41, 43, 45), features of the antennae (Figs 16, 51-53), and the copulatory pieces of the aedeagus (Fig. 3).

***Achilia nipponobythoides* n. sp.**

Figs 5, 15, 20, 28, 36, 38, 40, 54-56, 58

Holotype: MHNG (# MHNG-ENTO-13845); 1 ♂; SOUTHERN CHILI: Región Los Lagos: Osorno prov.: Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting.

Paratypes (3): SOUTHERN CHILI: Región Los Lagos: Llanquihue prov.: FMNH (FMHD #97-11); 1 ♂; Vicente Perez Rosales National Park, SW slope Volcán Osorno, km 10.1 to La Burbuja; 41° 08.30'S 72° 32.15'W; 925 m; 03-27.I.1997; A. Newton & M. Thayer 988; *Nothofagus dombeyi* & *Podocarpus nubigena* w/Valdivian rainforest understory, flight intercept trap. – Osorno prov.: FMNH; 1 ♂; Puyehue National Park, Antillanca road; 720-1000 m; 18-24.XII.1982; A. Newton & M. Thayer; *Nothofagus* ssp. forest, screen sweeping at dusk. – FMNH; 1 ♂; Vicente Perez Rosales National Park, N slope Volcán Osorno, road to Ref. La Picada; 41° 03.25'S 72° 30.18'W; 660 m; 16.XII.2002; A. Solodovnikov, A. Newton & M. Thayer 1067; *Nothofagus dombeyi* w/conifers dense *Chusquea* bamboo understory, flat area, Berlese, leaf & log litter.

Description: Body 1.45-1.60 mm long, reddish-brown, with darker abdomen, reddish elytra, antennae and legs, and yellowish palpi. Head with protruding eyes about as long as convex temples. Pronotum slightly wider than head; median antebasal fovea smaller than lateral ones. First abdominal tergite with basal striae extending to about one-third of paratergal length, and separated at base by about one-third of tergal width.

Male: Head as in Figs 36, 38 and 40; posterior part raised, slightly punctuate and pubescent; anterior part at middle

flattened, densely punctuate and pubescent, expanded just above eyes in two round shallow depression more densely punctuate and finely pubescent, and with strongly convergent anterior margins giving a triangular-shaped forehead; vertexal sulcus absent. Antennae (Figs 15, 54-56) with scape and pedicel distinctly longer than wide; antennomere III as wide as long; antennomere IV slightly wider than long; antennomere V slightly longer than wide; antennomere VI-VII wider than long with protruding lateral margins; antennomere VII transverse; antennomere VIII as wide as long; antennomere IX with mesal margin projecting in bilobed lamina with large apical setae; antennomere X strongly transverse, apical half of mesal margin projecting and bearing a tuft of setae, one of which particularly long and thin; antennomere XI elongate and longer than VIII-X combined, bearing long and thin subbasal seta inserted in deep impression. Metaventrite slightly raised at middle, this area with median depression. Legs with trochanters very elongate; protrochanters (Fig. 20) bearing tuft of setae; mesotrochanters (Fig. 28) unarmed; profemora and mesofemora slightly thickened; distal half of metatibiae slightly sinuate. Abdominal tergites unmodified. First abdominal ventrite with distinct median carina extending from posterior margin to about one-third of ventrite length. Aedeagus (Fig. 5, dorsal longitudinal struts not shown) 0.30 mm long; medial sclerites apically pointed, and associated on each side with one pointed sclerite.

Female: Unknown.

Collecting data: Collected in December and January in *Nothofagus* ssp. mixed forests by flight intercept traps and screen sweeping at dusk, and also by car netting and sifting.

Distribution: *Achilia nipponobythoides* n. sp. is known from Southern Chile (Fig. 58: blue triangles) only in the Region of Los Lagos (Llanquihue and Osorno provinces).

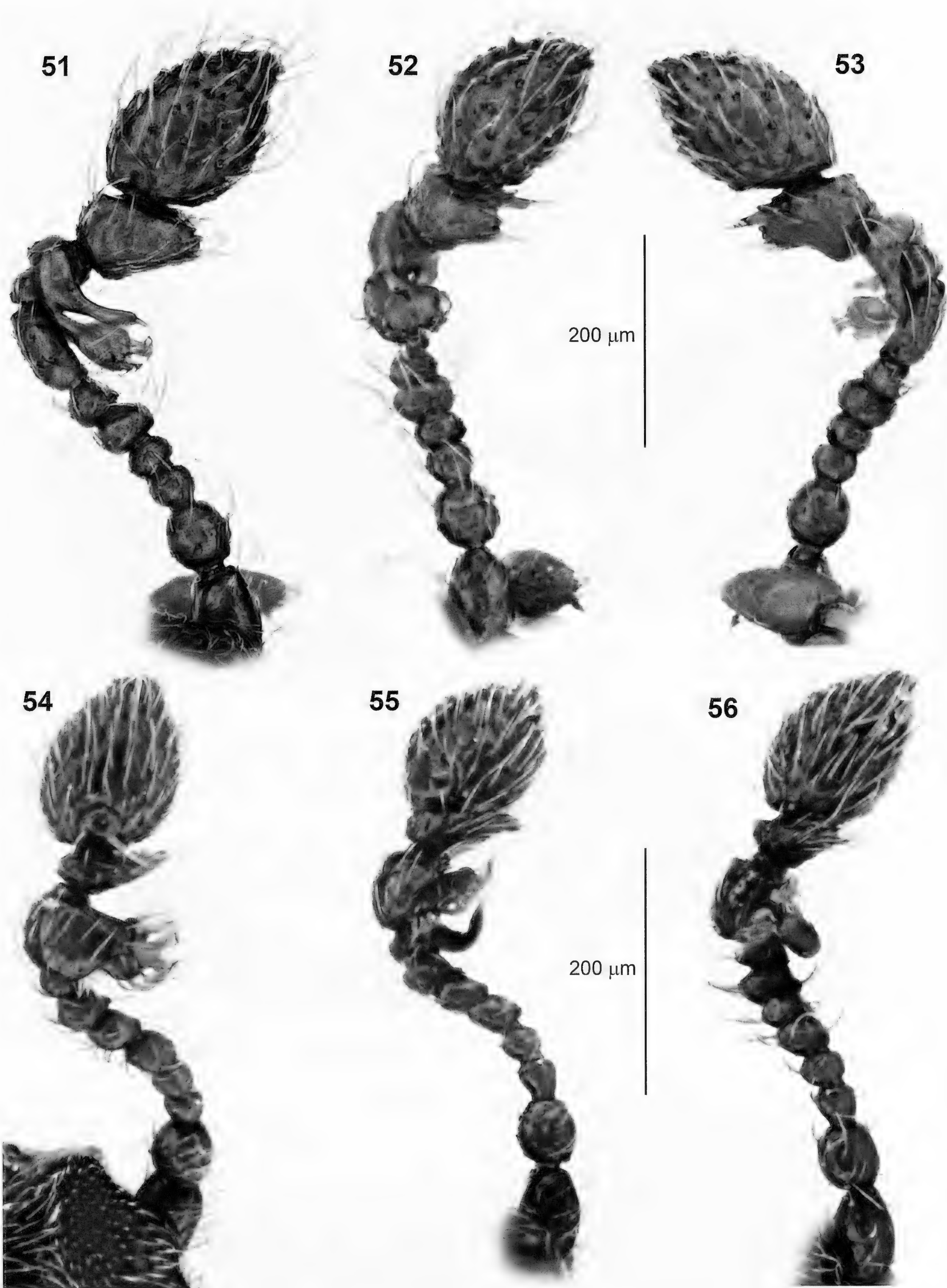
Comments: *Achilia nipponobythoides* n. sp. is easily distinguished from the other members of the genus by the very peculiar morphology of the male head (Figs 36, 38, 40), features of the antennae (Figs 15, 54-56), and the copulatory pieces of the aedeagus (Fig. 5).

***Achilia trulla* n. sp.**

Figs 6, 17, 24, 47-50, 58

Holotype: FMNH; 1 ♂; SOUTHERN CHILI: Región Los Lagos: Osorno prov.: Puyehue National Park, Antillanca road, site 659; 720 m; 18-24.XII.1982; A. Newton & M. Thayer; *Nothofagus* ssp. forest, flight intercept trap.

Description: Body 1.45 mm long, reddish-brown, with darker abdomen, and reddish elytra; antennae, palpi and legs yellowish. Head with weakly protruding eyes,



Figs 51-56. (51-53) *Achilia adorabilis* n. sp. (54-56) *A. nipponobythoides* n. sp. Male left antenna in (51, 54) dorsal, (55) oblique, (52, 56) frontal and (53) ventral views.

shorter than convex temples. Pronotum as wide as head; median antebasal fovea smaller than lateral ones. First abdominal tergite with basal striae extending to about one-third of paratergal length, and separated at base by about one-third of tergal width.

Male: Head as in Figs 47-48; frons with finely punctate and pubescent median depression with margins markedly raised and punctate, slightly expanded above eyes, the latter areas flattened and more densely punctate; anterior sides of head convergent. Antennae (Figs 17, 49-50) with scape and pedicel distinctly longer than wide; antennomere III as wide as long, antennomeres IV-V transverse; antennomere VI more than two times longer than wide with concave mesal margin; antennomere VII distinctly transverse; antennomere VIII transverse, its mesal margin projecting in large lamina; antennomere IX with mesal margin projecting in a long bilobed lamina bearing long and large apical setae; antennomere X strongly transverse, apical third of mesal margin projecting and bearing three long and thin setae; antennomere XI elongate and longer than VII-X combined, its surface with many tubercles. Metaventricle at middle slightly raised with faint median sulcus. Legs with trochanters very elongate; protrochanters bearing tuft of setae; ventral margin of mesotrochanters projecting posteriorly as short spine (Fig. 24); profemora and mesofemora slightly thickened; distal half of metatibiae slightly sinuate. Abdominal tergites and ventrites unmodified. Aedeagus (Fig. 6, dorsal longitudinal struts not shown) 0.30 mm long; medial sclerites apically pointed, and associated on each side with one pointed sclerite.

Female: Unknown.

Collecting data: Only one specimen collected in December in *Nothofagus* ssp. forest by flight intercept traps.

Distribution: *Achilia trulla* n. sp. is known only for the type locality in Region of Los Lagos (Osorno province) (Fig. 58: yellow stars).

Comments: *Achilia trulla* n. sp. is easily distinguished from the other members of the genus by the morphology of the male head (Figs 47-48), features of the antennae (Figs 17, 49-50), and shape of the aedeagus (Fig. 6).

Achilia zaurda n. sp.

Figs 8, 10, 18, 26, 42, 44, 46, 58

Bryaxis puncticeps. – Reitter, 1885: 324, 326 pl. II fig. 5 (head and antennae) (nec *Bryaxis puncticeps* Reitter, 1883).

Achilia puncticeps. – Jeannel, 1962: 414-415 (pro parte, description of male) figs 166 (habitus), 168 (aedeagus). – Kurbatov & Sabella, 2015: 304, fig. 63 (habitus).

Holotype: MHNG (# MHNG-ENTO-13846); 1 ♂; SOUTHERN CHILI: Región Los Lagos: Llanquihue prov.: Vicente Perez Rosales National Park, Salto Petrohué; 150 m; 23.XII.1984; S. & J. Peck; mixed forest litter, Berlese.

Paratypes (507): MNHN (ex coll. Raffray, sub *A. puncticeps*); 5 ♂; Chili. – SOUTHERN AND CENTRAL CHILI: Región Los Lagos: Llanquihue prov.: MHNG; 24 ♂ and 28 ♀; same data as holotype. – FMNH (FMHD #85-938, #85-54) 2 ♂ and 5 ♀; same data as holotype. – MHNG; 1 ♂; same data, but FIT. – FMNH (FMHD #85-939, #85-55); 1 ♂; same locality; 23.XII.1984/04.II.1985; S. & J. Peck; FIT mixed moist forest. – FMNH (FMHD #97-8); 4 ♂; Vicente Perez Rosales National Park, 9.2 km NE Ensenada, on road to Petrohué; 41° 10.20'S 72° 27.10'W; 125 m; 02-28.I.1997; A. Newton & M. Thayer 987; Valdivian rainforest w/*Nothofagus* ssp., flight intercept trap. – MHNG; 1 ♂; Frutillar Bajo, Universidad Chile Forest Reserve; 100 m; 22.XII.1984/02.II.1985; S. & J. Peck; FIT ravine mixed forest. – Chiloé prov.: MHNS (n. 1801); 1 ♂ (mislabelled as paratype of *Achilia monstrata chilota* n. 1801); Chiloé. – Osorno prov.: MHNG; 1 ♂; Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; D. Agosti & D. Burckhardt. – UNHC; 4 ♂; Puyehue National Park, Aguas Calientes; 440 m; 26.XII.1982; A. Newton & M. Thayer; Valdivian rainforest, at UV light. – FMNH; 4 ♂; same data. – MHNG; 1 ♀; Puyehue National Park, road Aguas Calientes-Antillanca, station 19b; 40° 45'S 72° 15-20'W; 750-850 m; 30.XI/01.XII.1992; D. Burckhardt; sifting of moss on tree trunks and forest floor and vegetational debris. – Región Araucanía: Cautín prov.: MHNG; 4 ♂; 15 km NE Villarrica, Flor del Lake; 300 m; 14.XII.1984/10.II.1985; S. & J. Peck; FIT *Nothofagus* forest. – MSNG; 2 ♂; Rio Pedregoso, Fundo Nueva Pomerania; TC-433; 25.I.1995; T. Cekalovic. – Región Bío Bío: Concepción prov.: FMNH; 62 ♂ and 137 ♀; Patagual; TC-369; 29.XI.1993; T. Cekalovic. – MSNG; 5 ♂ and 25 ♀; Puente Pelun; TC-358; 21.II.1993; T. Cekalovic. – MSNG; 32 ♂ and 154 ♀; Fundo El Manzano; TC-503; 17.XI.1996; T. Cekalovic. – MHNS; 2 ♂ and 2 ♀; same data.

Description: Body 1.50-1.60 mm long, entirely dark brown with reddish elytra darker at base and along sutural stria, or entirely reddish with darker head and sometimes abdomen, or entirely reddish, with legs and antennae reddish, and yellowish palpi. Head with protruding eyes, shorter than convex temples. Pronotum as wide as head; median antebasal fovea smaller than lateral ones. First abdominal tergite with basal striae extending to about one-third of paratergal length, and separated at base by about a one-third of tergal width.

Male: Head as in Figs 42, 44 and 46, posterior region raised in apically truncated and laterally rounded subconic median protuberance, the latter dorsally flattened and densely punctate; frontal lobe with convergent sides. Antennae (Fig. 18) with scape and pedicel longer than wide; all funicular antennomeres wider than long with antennomere VIII strongly transverse; antennomeres



Fig. 57. Distribution map. (● red circles) *Achilia puncticeps*. (▲ blue triangles) *A. cunniceps* n. sp. (◆ green diamonds) *A. reitteri* n. sp. (★ yellow stars) *A. adorabilis* n. sp.



Fig. 58. Distribution map. (● red circles) *Achilia zaurda* n. sp. (▲ blue triangles) *A. nipponobythoides* n. sp. (◆ green diamonds) *A. baburra* n. sp. (★ yellow stars) *A. trulla* n. sp.

IX two times wider than long; antennomere X very big, slightly wider than long, its surface with some tubercles; antennomere XI very elongate and distinctly longer than VI-X combined, its surface with many tubercles. Metaventrite raised at middle, this area punctuate and depressed; posterior margin densely covered with long backward bristles. Legs with trochanters elongates; ventral margin of mesotrochanters projecting at middle as spine (Fig. 26); profemora and mesofemora slightly thickened; distal third of mesotibiae (Fig. 10) sinuate and with long and thick bristles; its medial margin projecting as large and stout spur; distal half of metatibiae slightly sinuate. Abdominal tergites unmodified; surface of first abdominal ventrite raised and flattened at middle with distinct and stout median carina extending from posterior margin to more than third of ventrite length; second and third ventrites slightly flattened at middle; fourth abdominal ventrite hollowed at middle. Aedeagus (Fig. 8) 0.40-0.42 mm long with dorsal plate quadrangular with slightly sinuate sides, apical part narrowed and rounded; dorsal longitudinal struts divergent (not shown in Fig. 8). Copulatory pieces consisting of pair of long and large medially sinuated sclerites slightly enlarged apically and with pointed lateral margin; a robust spine-like process with distal third strongly curved laterally projects from middle of left sclerite, apex of this process bifid and forming two small spines directed ventrally. Parameres sinuate and bearing two short subapical setae, and two long spines directed ventrally and medially projecting from distal third.

Female: Similar to male except: head unmodified with frons slightly convex and with small vertexal fovea beside each eye, vertexal sulcus present. Antennae unmodified, with shorter and less thickened antennomeres, thinner than male; metaventrite, abdominal ventrites and legs unmodified.

Collecting data: Collected from November to February in Valdivian rainforests, *Nothofagus* ssp., and mixed forests, at elevations ranging from 100 m to 850 m. Most specimens came from sifted samples of leaf and log litter, moss, dead trunks, vegetable debris, and sometimes mushrooms, but also were collected by flight intercept traps and UV light.

Distribution: *Achilia zaurda* n. sp. is known from Southern and Central Chile (Fig. 58: red circles), ranging from Llanquihue to Concepción provinces.

Comments: The males of this species have been described and illustrated under the name *A. puncticeps* by Reitter (1885: 324, 326, pl. II, fig. 5) and Jeannel (1962: 414, figs 166-168). See also comments under *Achilia approximans* and *A. puncticeps* species groups, and under *A. puncticeps*.

Achilia zaurda n. sp. differs from all the other species treated above with respect to various characters, notably by the presence of two spines on the distal edge of the parameres. The structure of the aedeagus as well as the shape of the male head and antennae are diagnostic.

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